The Drivers of SOC Storage: the Effect of Climate, Forest Age, and Physicochemical Soil Properties in Swiss Forest Soils

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“Essentially, all life depends upon the soil . . . There can be no life without soil and no soil without life; they have evolved together.”

Charles E. Kellogg

“Occam’s Razor is the scientific principle that, all things being equal, the simplest explanation is always the dog ate my homework.”

Greg Tamblyn

SUMMARY

Soils are the largest terrestrial organic carbon reservoir. In particular, forest soils contain large stocks of soil organic carbon (SOC) and are assumed to contribute significantly to carbon sequestration over long periods of time. Even small changes in the SOC pool could have a highly significant impact on the balance of the global carbon cycle. Variations in climate, land-use changes, as well as, and the chemical and physical composition can affect SOC dynamics, and thus the uptake or release of CO_2 to the atmosphere. Understanding what the drivers of SOC storage are and the potential responses of SOC in a changing climate is therefore of a great importance for predicting climate change and prioritizing mitigation efforts.

The goal of my PhD project is to gain insight into soil organic matter (SOM) accumulated in Swiss forest soils and examine the controlling factors of SOC stocks. Specifically, my objectives were to: i.) assess the impact of forest age on SOC storage; ii.) to investigate the impact of climate (mainly characterized by mean annual temperature (MAT) and precipitation (MAP)) on SOC stocks and composition; iii.) to link SOC stocks to physicochemical parameters, known to stabilize SOM; and iv.) to compare measured and simulated SOC stocks using a litter decomposition model, and to identify the factors driving differences. The basis of my PhD project was the soil database of the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), containing information of over 1000 soil profiles distributed along the whole area of Switzerland therefore, comprising a large gradient in elevation, climate, and physicochemical soil properties.

Forest soils in Switzerland contain on average higher SOC stocks than temperate forests in other European countries with mean SOC stocks of 2.4 kg C m^{-2} and 10.9 kg C m^{-2} for the organic layer and mineral soil (at 0-120 cm soil depth), respectively. Changes in the land-use are associated with changes in both the formation and decomposition of SOC. In Switzerland, forest expansion has been the main land-use change, with a total areal increase of over 22% during the last century. We have estimated the minimal forest age of our sites using historical maps allowing the classification of three forest age classes (less than 60 years old, 60-120 years old, and at least 120 years old). Results revealed that the majority of the sites in the soil database had a forest cover for at least 120 years (n=567). Overall, the effect of forest age on SOC stocks was only minor and superimposed by the influence from climate, soil chemistry, and tree species composition. SOC stocks in the mineral soil were found to decrease with an increasing forest age ($12.5\pm0.9 > 11.4\pm0.5 > 10.5\pm0.3$ kg C m^{-2}, from the youngest to oldest forest sites). However, we attributed the apparent decrease primarily to a higher elevation of the young forested sites which had a higher MAP and MAP was positively related to SOC stocks, with an increase of 0.0081 kg SOC m^{-2} per mm. SOC stocks in the organic layer decreased with

an increase in MAT and were significantly higher under conifer trees as compared to under broadleaf ones (3.8 vs. 1.0 kg C m^{-2}). These findings suggest that the ongoing forest expansion in Switzerland would not likely contribute to further soil C sequestration.

The effects of climatic conditions on SOM were investigated by measuring SOC stocks and SOM composition along the natural elevational gradient in Swiss forests. Based on their density, distinct SOM fractions of 54 mineral soils (soil depth 0-20 cm) were separated into two light (free (fLF) and occluded (oLF)) and two heavy fractions (coarse and fine heavy fractions, cHF and fHF, respectively). The two light fractions represent the labile particulate organic matter (POM), whereas the two heavy fractions characterize the more stable mineral-associated organic matter (MOM). The corresponding organic layer was separated into L-F-H horizons. Roots found in the organic layer were added to the analysis. SOC stocks, C/N ratio, and isotope ratios of $\delta^{13}C$ and $\delta^{15}N$ were measured. We postulated that different climatic conditions will have a small effect on total SOC storage; however, we expected to find a pronounced effect of climate on SOM quality (expressed as the contribution of total POM to SOM stock and C/N ratio in terms of decomposability). The contribution of total POM (the sum of organic layer and POM fraction) to total SOM was highest in warm-moist climates (72.3%), whereas it was smallest in cold-moist climates (62.8%). In general, total POM contribution to total SOM contribution was higher than the MOM contribution, suggesting that a substantial part of the SOM pool is stored in a labile form. Smaller C/N ratios and higher $\delta^{15}N$ values are indicators for a greater SOM stability. The ratios of $\delta^{15}N$ relative to C/N decreased in the following order: fHF < cHF <fLF < oLF < roots, suggesting SOM stabilization in that order. Furthermore, we found that the organic layer only hardly contributes to the mineral-associated SOM pool. This is especially relevant for forest soils, where a substantial portion of particulate OM is stored in the organic layer, since it indicates that only a small part of the fresh C input will contribute to a long-term SOC storage.

The comparison of measurements and simulations of SOC stocks using the soil C model Yasso used for the Swiss greenhouse gas (GHG) reporting revealed a good agreement for three out of the five biogeographic regions in Switzerland. However, in the Jura and the Southern Alps, the SOC model systematically underestimated SOC stocks (ΔSOC = -4.1±0.6 and -9.9±1.5 kg C m^{-2}, respectively). The differences were primarily related to physicochemical soil properties and to a lesser extent to MAP. The Southern Alps are characterized by high contents of Fe- and Al-oxides, whereas the Jura has high contents of Ca-carbonates. These soil properties are known to bind SOM, thereby protecting it from decomposition. Moreover, SOC stocks were underestimated in areas with high MAP (ΔSOC = 0.5 kg C m^{-2} per 100 mm y^{-1}) and in waterlogged soils, strongly suggesting that a suppressed decomposition by anaerobic conditions is not represented by the model appropriately. Overall, these findings demonstrate that SOM stabilization plays a key role for SOM storage at the national scale, which, so far, has not adequately been accounted for in belowground C models.

In summary, this PhD thesis provides insights in the main driving factors of SOC storage in forest soils. This thesis also contributes to the improvement of soil C models to predict SOM responses to a future climate. This is in particular very relevant for Swiss GHG inventory reporting SOC stock changes. Though the results presented here are based on forest soils in Switzerland, an extrapolation to other temperate forest soils with similar climates and soil properties should be possible.

KURZFASSUNG

Die Böden sind der grösste terrestrische organische Kohlenstoffspeicher. Insbesondere Waldböden sind sehr kohlenstoffreich und tragen vermutlich zur langfristigen Kohlenstoff-Sequestrierung bei. Kleine Änderungen in den Vorräten an organischem Bodenkohlenstoff (SOC) könnten einen erheblichen Einfluss auf das Gleichgewicht des globalen Kohlenstoffkreislaufs haben. Die SOC-Dynamik wird durch verschiedene Faktoren beeinflusst, wie z. B. Klimaveränderungen und Landnutzungsänderungen, sowie durch die bodenchemische und physikalische Zusammensetzung. Um zu verstehen, wie diese Faktoren die Kohlenstoffabgabe und -aufnahme der Böden beeinflussen, ist es wichtig zu untersuchen, welches die steuernden Faktoren der SOC-Speicherung sind und wie diese auf ein sich änderndes Klima reagieren.

Meine Doktorarbeit hat zum Ziel, einen Einblick in die organische Bodensubstanz (SOM) in Schweizer Waldböden zu gewinnen, und die steuernden Faktoren der SOC-Vorräte zu untersuchen. Im Einzelnen waren meine Ziele: i.) die Auswirkungen des Waldalters auf die SOC-Vorräte zu ermitteln; ii.) die Auswirkungen des Klimas (bestehend überwiegend aus mittlerer jährlicher Temperatur (MAT) und Niederschlag (MAP)) zu untersuchen; iii.) die SOC-Vorräte mit physikalisch-chemischen Parametern zu verknüpfen, die zur Stabilisierung von SOM beitragen; und iv.) SOC-Vorratsmessungen mit Simulationen eines C-Models zu vergleichen und die Faktoren für Abweichungen zu identifizieren. Grundlage meiner Doktorarbeit war die Bodendatenbank der Eidgenössischen Forschungsanstalt für Wald, Schnee und Landschaft (WSL). Die Datenbank verfügt über Information von über 1000 Bodenprofilen, die auf dem gesamten Gebiet der Schweiz verteilt sind und daher einen großen klimatischen und physikochemischen Gradienten darstellen.

Die Waldböden in der Schweiz weisen höhere SOC-Vorräte als die temperierten Wälder benachbarter europäischer Länder auf. Im Mittel enthalten sie 2,4 kg C m^{-2} in der organischen

Auflage und 10,9 kg C m^{-2} im Mineralboden, die sich zwischen 0 bis in 120 cm Bodentiefe befinden. Landnutzungsänderungen beeinflussen den C-Eintrag und die Zersetzung von SOC. In der Schweiz stellt die Waldausdehnung die wichtigste Landnutzungsänderung dar; im letzten Jahrhundert hat die Waldfläche um über 22% zugenommen. Wir ermittelten das minimale Waldalter von unseren Standorten mittels historischer Karten. Diese Vorgehensweise erlaubte eine Klassifizierung in drei Waldaltersklassen (weniger als 60 Jahre alt, 60- bis 120-jährig und mindestens 120 Jahre alt). Es zeigte sich, dass die Mehrheit der Standorte in der Bodendatenbank ein Waldalter von mindestens 120 Jahren besaß (n=567). Das Waldalter wirkte sich nur geringfügig auf die SOC-Vorräte aus und wurde durch die Wirkung von Klima, Bodenchemie und Baumarten überlagert. Mit zunehmendem Alter nahmen die SOC-Vorräte im Mineralboden ab ($12{,}5 \pm 0{,}9 > 11{,}4 \pm 0{,}5 > 10{,}5 \pm 0{,}3$ kg C m^{-2}, von den jüngsten bis zu den ältesten Standorten). Wir schreiben diese Abnahme jedoch in erster Linie der höheren Lage der jüngeren Standorte zu, da die Niederschläge signifikant mit der Höhe zunehmen. Demgegenüber sanken die SOC-Vorräte in der organischen Auflage mit ansteigender Temperatur und waren unter Nadelbäumen signifikant höher als unter Laubbäumen (3,8 gegenüber 1,0 kg C m^{-2}). In der Gesamtheit deuten diese Ergebnisse darauf hin, dass die in der Schweiz laufende Waldausdehnung eher unwahrscheinlich zur Kohlenstoff-Sequestrierung in Böden beitragen wird. Um die Auswirkungen des Klimas auf die SOM zu verstehen, untersuchten wir die SOC-Vorräte sowie die SOM-Qualität entlang eines natürlichen Höhengradienten, der unterschiedliche klimatische Verhältnisse widerspiegelt. Mit Hilfe einer Dichtefraktionierung haben wir an 54 Standorten den oberen Mineralboden (0-20 cm) in leichte (freie (fLF) und okkludierte (oLF)) und schwere (grobe und feine, cHF und fHF) Fraktionen getrennt. Die zwei leichten Fraktionen stellten die partikuläre organische Substanz (POM), während die zwei schweren Fraktionen die mineralische organische Substanz (MOM) bildeten. Die entsprechende organische Auflage wurde in die L-F-H Horizonte aufgetrennt. Wurzeln, die in der organischen Auflage enthalten waren, wurden der Analyse hinzugefügt. Anschließend wurden die SOC-Vorräte, das C/N-Verhältnis und die Isotopenverhältnisse von $\delta^{13}C$ und $\delta^{15}N$ gemessen. Wir stellten folgende Hypothese auf: unterschiedliche klimatische Bedingungen werden einen geringeren Einfluss auf die gesamten SOC-Vorräte haben, jedoch eine starke Wirkung auf die SOM-Qualität. Letztere setzt sich aus dem Anteil des Gesamt-POM zum SOM und dem C/N-Verhältnis in Bezug auf die SOM-Zersetzbarkeit zusammen. Der höchste Anteil des Gesamt-POM (Summe der organischen Auflage und POM) am Gesamt-SOM unter warm-feuchten klimatischen Bedingungen (72,3%) beobachtet, während der niedrigste Anteil unter kalt-feuchtem Klima beobachtet wurde (62,8%). Der Gesamt-POM zum SOM-Anteil war höher als der MOM-Anteil, was darauf hindeutete, dass ein wesentlicher Teil des SOM-Vorrates in einer labilen Form gespeichert wurde. Niedrigere C/N und höhere $\delta^{15}N$-Verhältnisse sind Indikatoren für eine größere Stabilität der organischen Bodensubstanz. Die Verhältnisse von

$\delta^{15}N$ gegenüber C/N verringerten sich in der folgenden Reihenfolge: fHF < cHF < fLF < oLF < Wurzeln, was auf eine SOM Stabilisierung in dieser Reihenfolge hindeutet. Darüber hinaus stellten wir fest, dass die organische Auflage nur bedingt zum MOM beiträgt. Diese Erkenntnis ist besonders relevant für Waldböden, bei denen ein wesentlicher Teil der partikulären organischen Substanz in der organischen Auflage gespeichert wird, denn es weist darauf hin, dass nur ein kleiner Anteil des frischen C-Eintrages zu einer langfristigen SOC-Speicherung beitragen wird.

In einem weiteren Schritt wurden die Messungen von SOC-Vorräten mit Simulationen aus dem Boden-C-Model Yasso verglichen, welches im Schweizer Treibhausgasinventar verwendet wird. Im Ergebnis zeigte sich eine gute Einschätzung des Models für drei der fünf biographischen Regionen der Schweiz. Das Yasso-Model unterschätzte jedoch die SOC-Vorräte in zwei Regionen, namentlich Jura und Südalpen (ΔSOC=-4,1±0,6 und -9,9±1,5 kg C m^{-2}). Die Abweichungen wurden vor allem auf die physikochemischen Eigenschaften zurückgeführt, die im Model nicht berücksichtigt sind. In geringerem Maße trug auch der Niederschlag zu den Diskrepanzen bei. Die Südalpen zeichnen sich durch einen hohen Gehalt an Eisen- und Aliminium-Oxiden aus, während im Jura ein hoher Gehalt an Kalziumkarbonat vor kommt. Diese Bodeneigenschaften vermögen organische Bodensubstanz zu binden und sie so vor Zersetzung zu schützen. Des Weiteren zeigten die Ergebnisse, dass die Modellierung mittels Yasso bei hohen Jahresniederschlägen (0,5 kg C m^{-2} pro 100 mm a^{-1}) und in wasserstauenden Böden die SOC-Vorräte unterschätzt. Da das Model anaerobe Verhältnisse nicht berücksichtigt, könnte eine Kopplung an ein Bodenwasserhaushaltsmodel möglicherweise die C-Modellierung verbessern. Insgesamt zeigen die Ergebnisse, dass SOM-Stabilisierung eine zentrale Rolle für die SOM-Speicherung auf nationaler Ebene spielt, was jedoch bisher nicht adäquat in unterirdischen C-Modellen berücksichtigt wird.

Die vorliegende Doktorarbeit gibt einen Überblick über die wichtigsten Faktoren der SOC-Speicherung in Waldböden. Sie trägt zudem zur Verbesserung von Boden-Kohlenstoffmodellen bei, welche die Reaktionen der SOC-Vorräte auf den Klimawandel simulieren. Diese Erkenntnisse und Beiträge sind auch für das Schweizer Treibhausgasinventar relevant. Obwohl die hier gezeigten Ergebnisse auf Waldböden in der Schweiz beruhen, sollte eine Extrapolation zu anderen temperierten Waldböden mit ähnlichen Klimabedingungen und Bodeneigenschaften möglich sein.

CONTENT

LIST OF FIGURES (Parts A & C)

ABBREVIATIONS (Parts A & C)

Al – Aluminum

a. s. l. – Above sea level

BC – Base cations

C – Carbon

Ca - Calcium

CEC – Cation exchange capacity

cHF – Coarse heavy fraction

CO_2 - Carbon dioxide

$\delta^{13}C$ – Stable isotope ratio of C (delta notation)

$\delta^{15}N$ - Stable isotope ratio of N (delta notation)

DEM – Digital elevation model

Fe- Iron

fHF – Fine heavy fraction

fLF – Free light fraction

GHG – Greenhouse gas

HF –Heavy fraction

OM – Organic matter

oLF – Occluded light fraction

LF – Light fraction

MAP – Mean annual precipitation

MAT – Mean annual temperature

MOM – Mineral-associated organic matter

Pg - Petagrams (10^{15} g)

POM – Particulate organic matter

ppm – Parts per million

SE – Standard error

SOC- Soil organic carbon

SOM – Soil organic matter

vs – Versus

Part A: SYNOPSIS

1. GENERAL INTRODUCTION

1.1. Importance of the global carbon cycle for the terrestrial carbon cycle

Concentrations of greenhouse gases (GHG) have been continually and steadily increasing since the beginning of the industrial revolution causing the observed warming by 0.85°C (IPCC, 2014). Carbon dioxide (CO_2), the most abundant and important GHG gas is constantly exchanged between four major carbon reservoirs: the atmosphere, the terrestrial biosphere (above- and belowground), the oceans, and the lithosphere. CO_2 is removed from the atmosphere by plant photosynthesis, during which carbon is fixed by the plants and cycled through soils and finally it is released by plant and soil microbial respiration back into the atmosphere (*Fig. 1*).

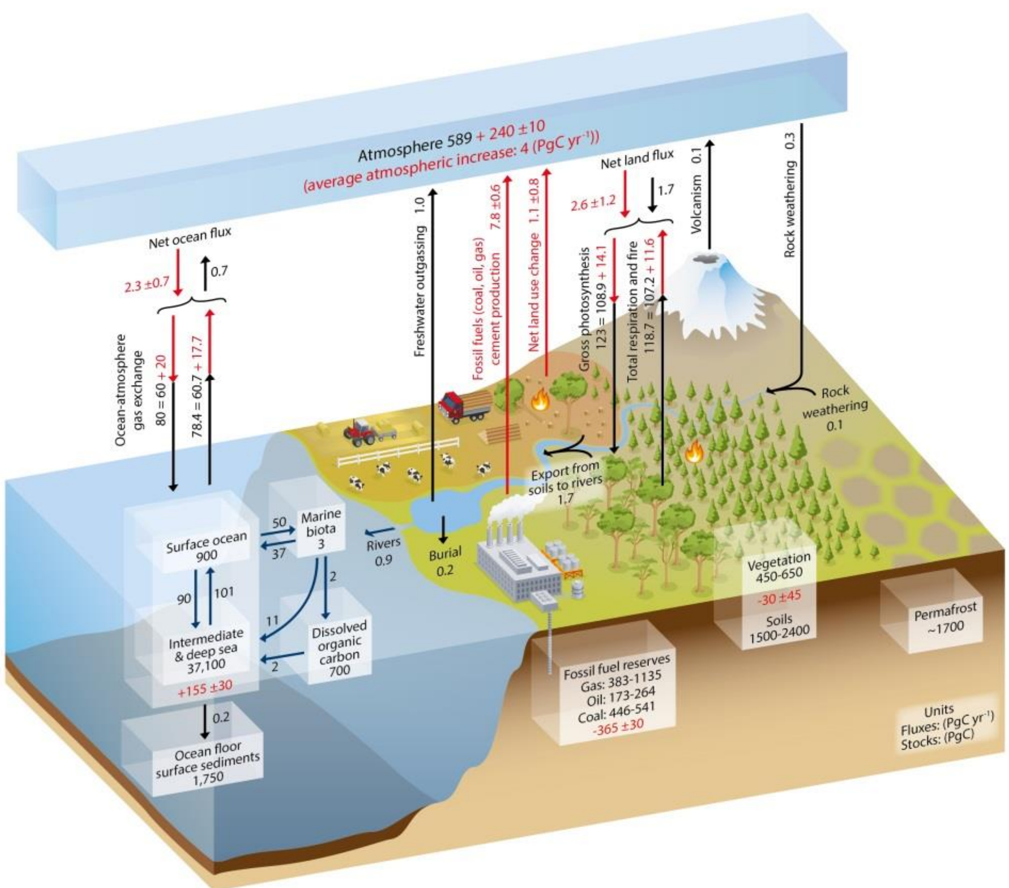

Fig. 1: The global carbon cycle illustrated as carbon stocks and carbon fluxes. Boxes represent the carbon stocks (in Pg C). Arrows denote annual carbon fluxes (in Pg C yr^{-1}). Levels of preindustrial fluxes and stocks are shown in black, anthropogenic ones are shown in red. Figure is reproduced from Ciais et al., (2013).

Two key anthropogenic activities, recognized to exert the strongest impact on the carbon cycle by releasing CO_2 emissions into the atmosphere, are fossil fuel burning and land use changes (Ciais et al., 2013). The current concentration of CO_2 is 409.98 ppm (20th May 2017, (NOAA, 2017)), which corresponds to a mass of approximately 873 Pg C (1 Pg=10^{15}g). Whereas IPCC predictions reveal a continuation of the uptake of anthropogenic carbon by the oceans, there are high uncertainties regarding the magnitude and the direction of changes in the uptake of terrestrial carbon (Ciais et al., 2013).

Soils are the largest terrestrial organic carbon reservoir (Lehmann and Kleber, 2015; Bradford et al., 2016). Globally, they store approximately 1,600 Pg of C, which is twice as much as the carbon stored in the atmosphere and thrice as much as in the vegetation (600 Pg C) (Batjes, 1996). Therefore, even small changes in the soil organic carbon (SOC) pool could have a significant impact on the balance of the global carbon cycle and CO_2 concentrations into the atmosphere (Smith et al., 2008a; Bradford et al., 2016). Understanding what the controls of SOC storage are and the potential responses of SOC in a changing climate is therefore of a great importance. Even though basic C cycle processes are well understood and despite the existing ongoing research in the area, there is no consent yet on the soil C balance and which factors are causing changes.

1.2. Soil Organic Matter (SOM) functions

Soil organic matter (SOM) is a continuum of compounds in different stages of decomposition, ranging from fresh plant and animal residues to entirely degraded matter (Blume et al., 2016). In addition to their degree of decomposition, their turnover time varies from months for biologically active soils, to millennia for soils with a very long mean residence time, which are stabilized and thus resistant to mineralization (*Fig. 2*). The decomposition rates and mean residence time of SOM depend on various chemical, biological and physical processes (Schmidt et al., 2011; Blume et al., 2016).

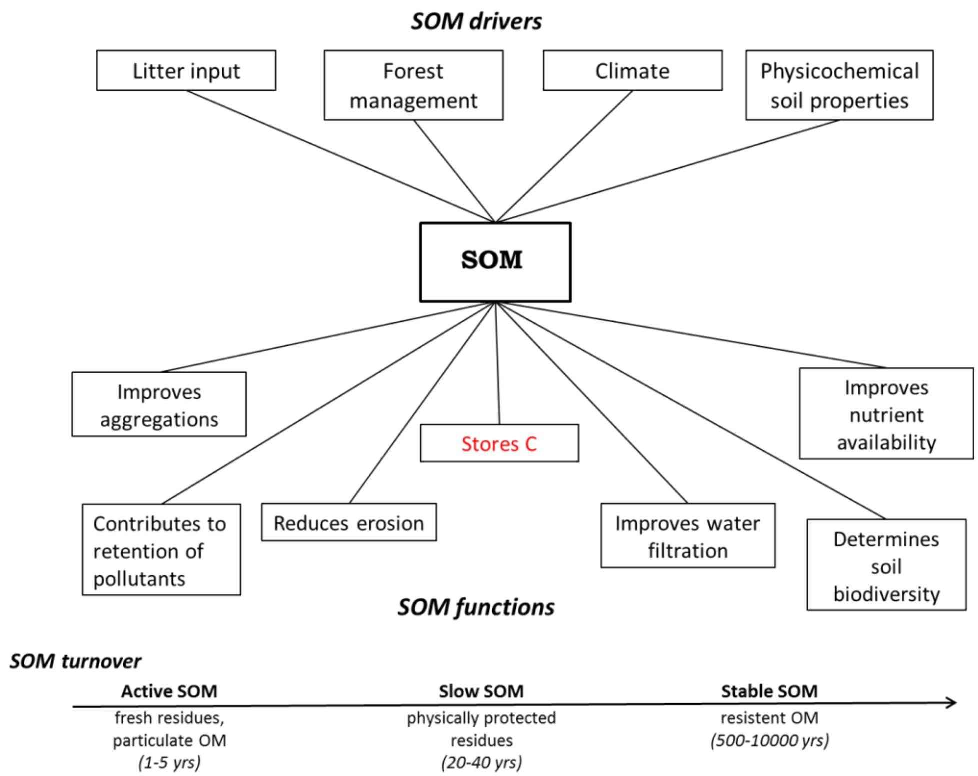

Fig. 2: A schematic of the main SOM drivers, the main SOM functions, and turnover time of SOM. Figure is reproduced from FAO (2004).

SOM also affects various biological and physicochemical soil properties. For example, SOM is the main source of energy for the soil fauna and microflora. Furthermore, it is a vital nutrient source and determines soil biodiversity, and has also an impact on chemical and physical soil properties, causing for instance an increase in the cation exchange capacity (Powlson et al., 2015). A central role that SOM plays, however, is storing C.

1.3. Carbon dynamics in forest soils

Forest soils are particularly carbon-rich and can contribute to a significant decrease of atmospheric CO_2 (Lorenz and Lal, 2010; Lal and Lorenz, 2012). To a certain degree, the large carbon storage in forest soils is due to the continuous litter input coming from the continual tree biomass production which has accumulated over millennia (Smith et al., 2008a). Presently forest soils in Europe, and temperate forest soils in particular, are assumed to be a carbon sink (Nabuurs et al., 2003; Ciais et al., 2008; Luyssaert et al., 2010; Pan et al., 2011) as a result of an increase of forest biomass density or reductions in harvest, leading to higher C inputs into soils (Pan et al., 2011). Moreover, forest expansion has taken place in Europe since the 50s of the last century.

Swiss forests have been managed by harvest on small areas only ("Femel-Schlag"), which means that no intensive management has taken place in these forests. This near-nature structure in combination with favorable climatic conditions (cool and humid conditions) have resulted into higher SOC stocks in Swiss forests compared to other European temperate forest soils (for the Swiss carbon cycle, please see *Fig. 3*; for a comparison of SOC stock estimations at soil depth 0-20 cm, please see Liski et al., (2002). In particular, the Southern Alps contain very high SOC stocks (nearly 180 t C ha^{-1}, in the organic layer and mineral soil down to 120 cm soil depth), which can partially be explained by high amounts of black carbon found there but also by Fe- and Al- oxides, acting as stabilizers of SOM (Eckmeier et al., 2010). Generally, SOC stocks increase with altitude and are higher in mountainous regions due to the colder temperatures (Hagedorn et al., 2010a).

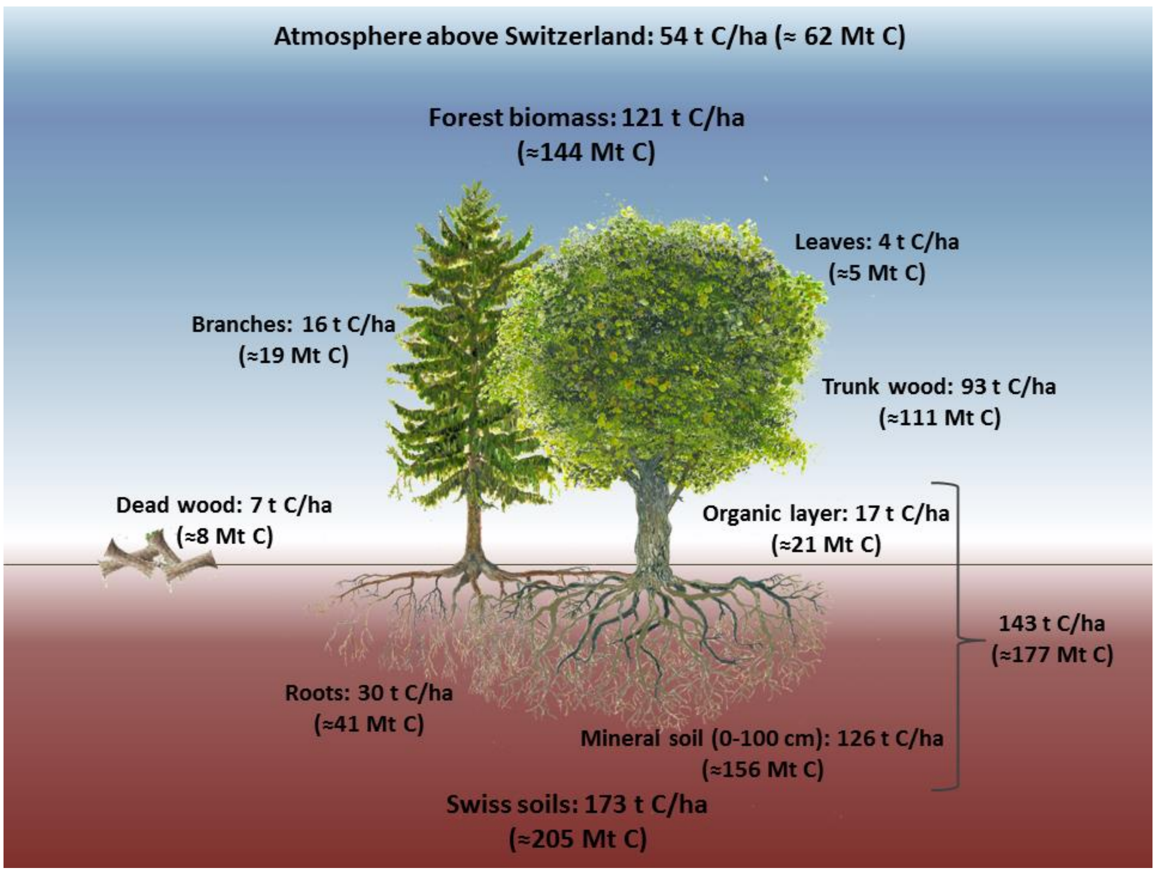

Fig. 3: Graphical representation of the Swiss carbon cycle. Figure modified from Frank Hagedorn, credit tree drawings: Hanspeter Läser. Values are based on the latest forest report (Waldbericht) for Switzerland, values in parenthesis show total C stocks (Rigling and Schaffer, 2015).

In Switzerland, forest SOC stocks increase with 4.3 t C ha^{-1} per 100 m and soils located above 1200 m a. s. l. store approximately 20 t C ha^{-1} in their organic layer more than those below this elevation (Sjögersten et al., 2011). Furthermore, conifer forests store more C in the organic layer as compared to broadleaf ones (38.0±2.4 vs. 10.1±0.7 t C ha^{-1}). In comparison, there is no significant difference in SOC storage in the mineral soil (*Fig. 4*). In the last century, a pronounced forest expansion has taken place in Switzerland, similar to other Central European countries. Swiss forest areas have increased by approximately 22%, primarily at the expense of alpine grasslands (Brändli, 2010). Currently, approximately one-third of the country's area is covered by forests (1.28 million ha), with the greatest percentage of forest area in the region of the Southern Alps and the smallest – in the Swiss Plateau (Brändli, 2010). Newly afforested soils have the potential to become C sinks, due to augmented biomass production and a larger rooting system resulting in greater C input into the soils (Lorenz and Lal, 2010; Fuchs et al., 2016). However, the previous land-use is of enormous importance as certain land-uses such as grasslands contain similar or higher SOC stocks to forest soils, whereas croplands contain lower ones (Guo and Gifford, 2002). Therefore, knowledge on the previous land-use is imperative in obtaining an accurate estimation of the SOC stock change following forest expansion.

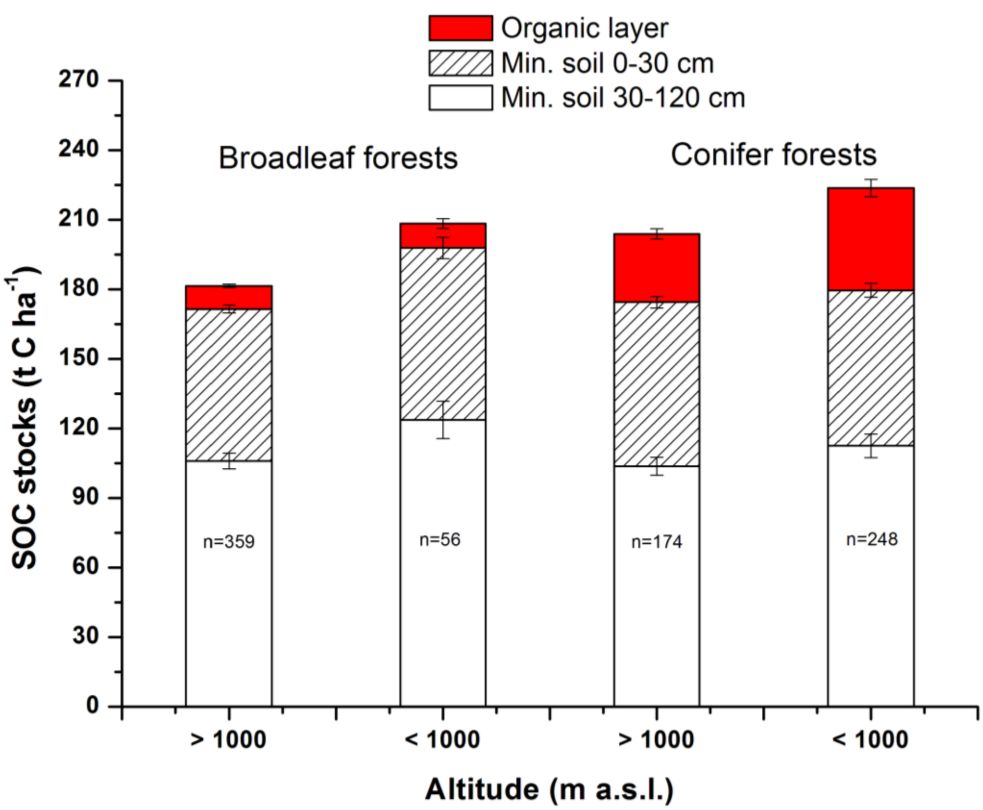

Fig. 4: Effect of forest type (broadleaf and conifer) on SOC storage (organic layer and mineral soil at 0-30 and 30-120 cm soil depths) according to altitudinal classes (below and above 1000 m a.s.l.). Error bars represent standard errors for the single horizons (WSL soil data base).

2. DRIVERS OF SOC STOCKS AND DYNAMICS

Soil organic carbon (SOC) storage is determined by the balance between the in- and outputs of carbon to the soil. Carbon (C) inputs reflect the transformation and stabilization of carbon into the soil layers, whereas C outputs are represented as the losses of C respired back to the atmosphere in the form of CO_2. The rates at which C is being stabilized and thus sequestered, as opposed to respired back to the atmosphere and the balance between these is crucial for soils functioning as either C sinks or C sources. These processes are controlled by diverse factors such as plant litter inputs, climate conditions, land use, and soil properties. Their quantitative and qualitative importance is not yet well understood and it therefore needs further exploration.

2.1. Plant litter inputs and tree species composition

SOM formation, its decomposition, and the storage of SOC are driven mainly by plant inputs into the soil (Paul, 2016). Tree species composition influences the quality of the litter input into the soils, which furthermore affects the quality and the content of SOC (Goldhaber and Banwart, 2015). SOM decomposition rates differ according to the fresh plant-derived inputs to the soil. Based on the turnover time, SOM can be divided into a labile, more readily decomposable fraction, with a short turnover time of a few weeks to a few years, and a more resistant, stable carbon, with a longer turnover time of a few years to decades. Regardless of the turnover time, once the litter has entered the soil it begins to decompose. Very recently, it was suggested that the interaction between litter chemistry and soil mineral properties regulates to a large extent the potential of SOC sequestration (Tamura et al., 2017). In general, new litter input should contribute to the SOC storage. Studies, however, suggest that inputs of fresh litter into the soil would stimulate the mineralization of older more stable carbon by 'priming' (Fontaine et al., 2004, 2007).

2.2. Climate

Climate is considered to be one of the most important drivers of SOM process rates and thus potentially also of SOC stocks (Smith, 2008b; Smith et al., 2015). Since microbial activity is temperature and moisture dependent, climatic changes will affect soil carbon cycling (Jobbágy and Jackson, 2000; Hagedorn et al., 2010a). With warmer climate, microbial decomposition of SOM is expected to increase (Crowther et al., 2016), resulting in carbon release into the atmosphere (Bradford et al., 2016). However, simultaneously, a warmer climate is typically associated with an increased litter input into the soils, leading to additional inputs of SOM. It is unclear whether increasing temperatures would lead to an enhanced SOC mineralization, to a greater SOM sequestration, or to a new carbon balance where larger litter inputs would be offset by an increased microbial decomposition. Furthermore, precipitation regimes have been projected to change towards a more intra-annual cycle with less frequent but more intense precipitation events interrupted by longer drought periods (Knapp et al., 2008). Such changes could influence the water regime and moisture levels of soils, hence, affecting decomposition rates of SOM (Hartmann et al., 2017). Furthermore, extended drought periods could reduce CO_2 assimilation by plants, therefore decreasing C input into soils (Hagedorn et al., 2016). For mountainous countries, such as Switzerland, changes in mean annual temperatures are of a great importance, since high-elevation ecosystems, known to contain more labile SOM (more easily decomposable SOM) as lower elevations (Leifeld et al., 2009; Hagedorn et al., 2010a), are going to be more susceptible to increasing temperatures. Mean annual temperatures have increased more strongly in Swiss alpine regions as compared to the rest of Europe (Hagedorn et al., 2010c), making the large amounts of labile SOC potentially vulnerable. For example, a soil warming experiment observed instantaneous soil C losses in a Swiss alpine treeline ecosystems (Hagedorn et al., 2010b). Based on a repeated soil survey, Prietzel et al., (2016) reported climate warming-induced OM losses in Bavarian soils in Germany, which have similar climate and topography as Switzerland. Nonetheless, there are still considerable uncertainties regarding the impact of climatic changes on the composition and turnover of SOC stocks. Considering the longer time periods necessary for SOC responses to become evident and the enormous spatial heterogeneity of soils, predicting the extent of the terrestrial feedback on SOC storage in soils will remain difficult.

2.3. Land use change

Land use changes can strongly affect soil properties and soil functions (Hiltbrunner et al., 2012, 2013; Fuchs et al., 2016; Deng et al., 2016). In addition to affecting SOC quantity, land management can have long-lasting impacts on SOM quality, as well as, increase bulk density, soil erosion and runoff (Hiltbrunner et al., 2012). Since soils store the largest carbon pools in forest ecosystems (Pan et al., 2011), disturbances due to land use changes can turn these into carbon sources (Achat et al., 2015). It has been generally accepted that SOC losses occur when forests and grasslands are converted to croplands (Poeplau et al., 2011). SOC tends to be re-gained when afforestation or restoration of native vegetation takes place on cropland (Guo and Gifford, 2002; Smith, 2008; Joosten, 2015). The ongoing expansion of forest areas observed in Europe since the 50 years of the last century (Janssens et al., 2003; Kümmerle et al., 2015) is regarded as a major land use change. For Switzerland, Ginzler et al., (2011) reported an increase of nearly 22% of forest area in the last century, resulting in one-third of the total country’s territory being covered in forests. Examining the effect of the current forest expansion is therefore essential to monitoring the drivers of SOC storage and dynamics.

2.4. Physicochemical soil properties

The ability of soils to stabilize organic matter, therefore protecting it from decomposition, influences greatly the dynamics of soil carbon. The persistence of organic matter (OM) in soils depends on numerous ecosystem properties (Schmidt et al., 2011), since it is stabilized in soils via different physical, biochemical, and physicochemical mechanisms (von Lützow et al., 2007). Physical stabilization refers to the occlusion of SOM in aggregates, protecting these from decomposer organisms (Six et al., 2002). Biochemical stabilization refers to the selective preservation of more recalcitrant compounds (Preston and Schmidt, 2006; Marschner et al., 2008). The third mechanism refers to the interaction between SOM and mineral surfaces; soil mineralogy is therefore considered an important determinant of the quantity of OC stored in the soil (Torn et al., 1997; Kaiser and Guggenberger, 2003; Spielvogel et al., 2008). Once organic matter is stabilized in soils, it can persist in soil for thousands of years (van der Voort et al., 2016), contributing therefore to long-term SOC sequestration. If disturbed (e.g. due to changes in environmental conditions or land use changes), SOM can be destabilized, mineralized and released in the atmosphere in the form of CO_2, becoming therefore, a C source. Recently, however, the SOM stabilization paradigm has been challenged, introducing the concept of persistence of OM in soils as an ecosystem property (Schmidt et al., 2011). Lehmann and Kleber, (2015) extended the concept further suggesting SOM to be in a continuous turnover process of organic compounds dependent on the microbial accessibility of SOM. Furthermore, both studies suggest that an interdisciplinary approach combining theoretical and practical methods will improve our understanding of SOM processes and mechanisms (Schmidt et al., 2011; Lehmann and Kleber, 2015).

3. AIMS AND OBJECTIVES

Considering the key importance of SOM for numerous soil functions (*Fig. 2*), the goal of this thesis was to identify the main drivers of SOC storage in forest soils in Switzerland. Specifically, my objectives were to 1) investigate the effect of historical land use change on SOC stocks; 2) assess the impact of tree species composition on SOM stocks; 3) estimate the impact of climate and physicochemical soil properties on SOC stabilization; 4) investigate the effects of climate on SOM quality; and 5) to analyze the discrepancies between measured and modeled SOC stocks using the litter decomposition model Yasso to unravel the major environmental parameters controlling SOC storage.

In particular the following questions were addressed:

3.1. Historical land use change

- *To what extent does the ongoing forest expansion in Switzerland affect SOC stocks?*
- *How important is forest cover age as compared to climate, vegetation, and soil properties?*

3.2. Distribution of SOM along climatic gradients

- *How does SOC stocks vary along climatic gradients in Switzerland?*
- *Does climate have a prominent effect on SOM quality?*

3.3. Disentangling the drivers of SOC stocks: a model based analysis of the Swiss soil inventory

- *How well does the litter decomposition model Yasso15 predict SOC stocks in Swiss forest soils?*
- *Can physicochemical soil properties explain the discrepancies between measured and modeled SOC stocks?*

4. MATERIALS AND METHODS

4.1. WSL Soil database

This PhD project was based on the evaluation of a large soil database, collected by and stored at the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL). The database comprises of over 1000 soil sites collected in the past 45 years, from which the oldest soil profile dates back to 1972. Information on the soil profiles is available according to soil horizons as well as by soil depth. The soil sites were collected in a manner to cover the whole forested territory of Switzerland, having therefore a large spatial coverage (*Fig. 5*). In addition to information on soil profiles, the database contains information on C and N concentrations, physical and chemical soil properties, topography, climate, and vegetation. The elements of this database most valuable for the purposes of this PhD thesis are described in detail below.

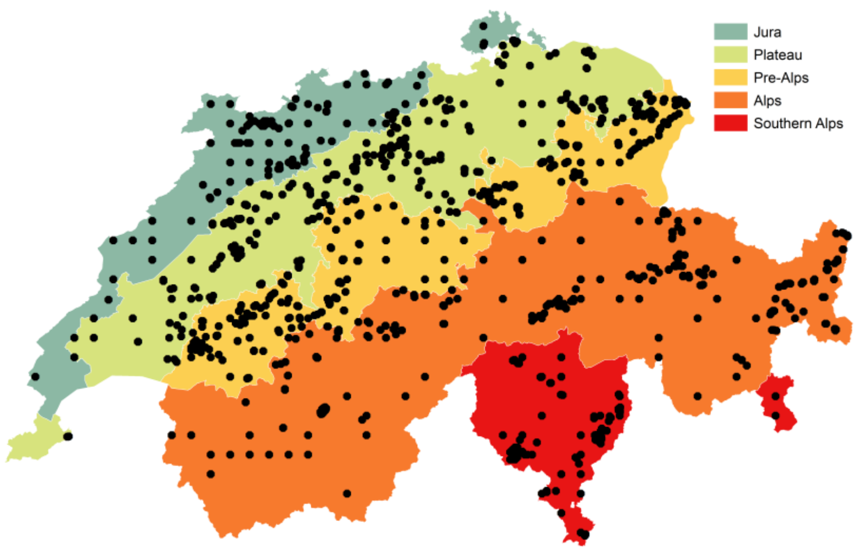

Fig. 5: Distribution of forest soil samples according to Swiss biogeographic regions

4.1.1. Soil data

The morphology of all collected soil profiles was determined and samples were collected by genetic horizons, either down to 120 cm soil depth on average or to parent rock. Samples were dried at 40-60°C and sieved with a 2 mm mesh prior to chemical analysis. Humus forms were classified into: mull (L horizon present), moder (L + F horizon present), and mor (L+F+H horizons present). Soil type was classified according to the World Reference Base (IUSS Working Group, 2007) and for the purposes of this PhD project, soil types were grouped into calcareous, acidic, and waterlogged soil groups. Calcareous and acidic soils were separated according to the criterion of existence of lime in the fine earth fraction (< 2 mm) at a decalcified soil depth of one meter. Waterlogged soils comprised of Gleysols and Stagnosols. Rooting depth was assessed directly in the soil pits.

Soil pH was measured in 0.01 M $CaCl_2$. Exchangeable cations of Al, Ca, Fe, K, Mg, and Na, effective cation exchange capacity (CEC), as well as, basic cation contents (BC), comprising the sum of the exchangeable basic cations (Ca, Mg, K, and Na), were determined by extraction with unbuffered 1 M NH4Cl (soil:solution = 1:10, end-over-end shaker for 1 hour) and measured by an ICP-OES (Perkin Elmer Optima 7300DV) according to Walthert et al., (2013). The mean contents were calculated for different soil depths by weighting the averages of the contents with the amount of fine earth. Clay, silt, and sand contents of 600 sites were measured with the sedimentation method according to (Gee and Bauder, 1986). Field estimates, according to 10 soil texture classes, were used for the rest of the samples (Walthert et al., 2004).

4.1.2. Climate and topography

Climate data were based on the Swiss meteorological network MeteoSwiss combined with suitable interpolation methods. Mean annual precipitation (MAP) and temperature (MAT) for the period 1981-2010 were provided by Meteotest (Remund et al., 2014). Altitude and slope were determined from a 25-m digital elevation model (DEM, Swisstopo, 2011). Exposition and relief were measured directly at the soil pit according to their position in the field (e.g., North-West for exposition and hilltop for relief) and categorized into groups according to the purpose of the studies (see *Paper III*).

4.1.3. Vegetation and forest cover age

Plant species in herb, shrub and tree layers were determined using the Braun-Blanquet cover abundance scale (Braun-Blanquet, 1964). The broadleaf percentage was calculated as the sum of the cover of all broadleaf species divided by the sum of the cover of all tree species at canopy level. Forest type was subdivided into two classes: coniferous (0-50%) and broadleaf (51-100%) forests. Forest cover change was estimated using historic and modern topographic maps. Accordingly, the minimal forest age could be estimated for the majority of the sites (n=857). For a more detailed description of the forest cover age estimation, please see *Paper I*.

4.1.4. SOC stocks calculation

Total and organic C contents were measured in ground samples by dry combustion using a C/N analyzer NC 2500 (CE Instruments, Italy). Inorganic C in samples with a pH > 6.0 was removed with acid vapor prior to analysis (Walthert et al., 2010). SOC stocks were calculated for the organic layer and the mineral soil at different soil depths. Total SOC stocks were represented by the sum of SOC stocks in the organic layer and mineral soil at depth 0-120 cm.

The SOC stock in the organic layer was calculated according to Moeri, (2007), where the mass of the organic layer was calculated as the product of the density (L: 0.10 g/cm^3, F: 0.15 g/cm^3, H: 0.20 g/cm^3) and the volume (based on measured thicknesses), which was then multiplied with its C concentration. SOC stocks in the mineral soil were calculated using equation (1):

$$SOC_{hz} = \sum_{i}^{z} (h_i \, (1 - \theta_i) \, \rho_i \, C_i) \qquad (1)$$

where SOC_{hz} is the SOC stocks of all horizons hz (kg C m^{-2}), Ci is the carbon concentration of the horizon i (kg kg^{-1}), ρi is the density of the fine earth (g cm^{-3}), θi is the volumetric stone content (m^3 m^{-3}), and hi is the horizon thickness (m). Fine earth density was estimated with a pedotransfer function, based on a calibration dataset of 559 mineral soil horizons from 134 different sites and a validation set of 131 horizons from 34 sites (Nussbaum et al., 2016). The pedotransfer function relied on the SOC content, the square root of the sampling depth, the square root of the slope, the skeleton content, three field density estimates, and 9 physiographical unit categories. Finally, SOC stocks were corrected for the position of the slope by multiplying them with the cosine of the slope.

Generally, most existing studies concentrate on the top soils (0-30 cm soil depth), therefore neglecting the deeper SOM pool distribution. The soil database used in this PhD project is therefore a unique tool as it comprises information not only on soil physicochemical parameters but on SOC stocks to a soil depth of 0-120 cm or to the parent material. This enabled analyses representative for the entire soil profile. Furthermore, given the size and spatial distribution of the soil profiles, the results of this PhD project cover a large climatic and topographic gradient.

4.2. Methods

Within this PhD thesis, three different approaches were used to investigate the drivers behind SOC storage in Swiss forest soils (*Fig. 6*).

The historical approach. Firstly, the impact of forest age on SOC stocks was investigated. For this, historic and modern topographic maps were used to determine the minimal forest age of 857 sites. Thereafter, the impact of forest age in combination with other parameters, such as climate, topography, and soil chemistry and texture, were studied via statistical analysis (*Paper I*).

The quality approach. The second approach included a subset of 54 sites, selected according to an ecosystem variability procedure. The organic layer was separated into horizons (L-F-H), whereas for the mineral soil (at soil depth 0-20 cm) density fractionation was used to separate the fractions into light and heavy. In addition to calculating SOC stocks and C/N ratios for the individual fractions, isotopic ratios of $\delta^{13}C$ and $\delta^{15}N$ were measured and included in the analysis. Subsequently, the distribution of SOM pools along four climatic gradients was studied (*Paper II*).

The modeling approach. The third approach included a comparison between measurements and simulations of SOC stocks of 564 forest sites. The latest version of the litter decomposition model Yasso (Yasso15) was used to simulate SOC stocks based on the coordinates of the corresponding forest soil sites available in the WSL soil database. A measured-modeled residual analysis was performed to test whether physical and chemical soil properties known to stabilize SOM but not included in Yasso can explain the discrepancies (*Paper III*).

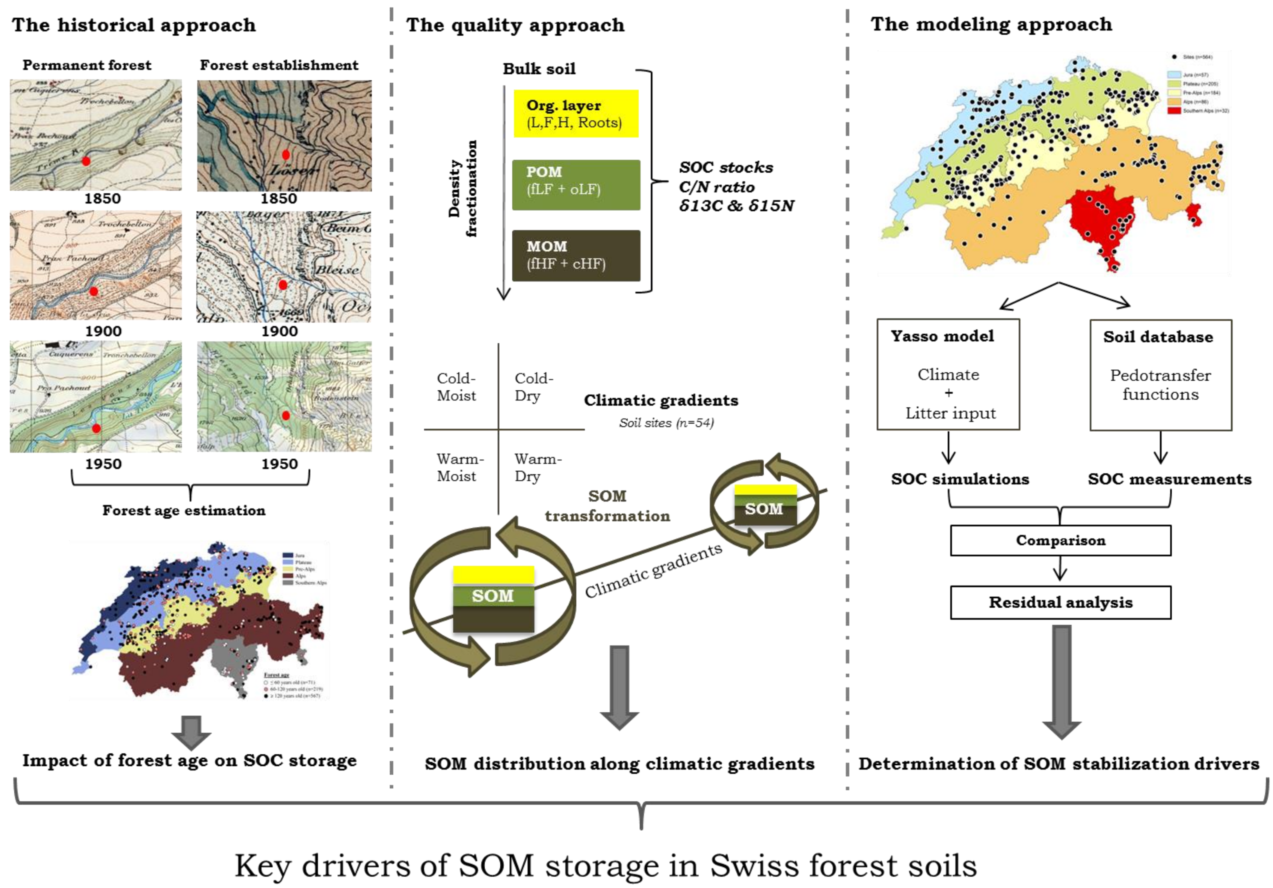

Fig. 6: PhD thesis methodology

Part B: PUBLICATIONS

Paper I

Reconstruction of historic forest cover changes indicates minor effects on carbon stocks in Swiss forest soils

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ABSTRACT

Forest cover in Switzerland and other European countries has gradually increased in the past century. Our knowledge of the impacts of forest expansion and development on soil organic carbon (SOC) storage is, however, limited due to uncertainties in land-use history and lack of historical soil samples. We investigated the effect of forest age on current SOC storage in Switzerland. For 857 sites, we analyzed SOC stocks and determined the minimal forest age for all presently forested sites using digitized historical maps, classifying all sites into three categories: young (≤60 years), medium (60–120 years), and old (≥120 years) forests. Grassland was the primary previous use of afforested land. Forest age affected current SOC stocks only moderately, whereas climate, soil chemistry, and tree species exerted a stronger impact. In the organic layer, highest SOC stocks were found in medium sites (3.0±0.3 kg C m^{-2}). As compared to other age categories, these sites had a 10% higher cover in coniferous forests with higher organic layer C stocks than broadleaf forests. SOC stocks in mineral soils decreased with increasing forest age (12.5±0.9, 11.4±0.5, 10.5±0.3 kg C m^{-2}). This decrease was primarily related to a 200-m higher average elevation of young sites and higher SOC stocks in a colder and more humid climate. In summary, forest age has only a minor effect on SOC storage in Swiss forest soils. Therefore, ongoing forest expansion in mountainous regions of Europe is unlikely contributing to soil C sequestration.

Key words: carbon sequestration; land use; land use history; forest age; minimal forest age; forest expansion; soil organic matter; soil organic carbon; Swiss forest soils.

1. INTRODUCTION

Soils represent the largest carbon (C) reservoir in terrestrial ecosystems (Schmidt and others 2011; Scharlemann and others 2014)—globally, the quantity of soil organic carbon (SOC) is about three times larger than the amount stored in vegetation and twice as much as in the atmosphere (Ciais and others 2013). Forest soils are particularly carbon-rich (Lorenz and Lal 2010) and therefore imperative when considering carbon storage for greenhouse gas (GHG) inventories. Land-use change (LUC) alters C storage in biomass as well as in soils (Guo and Gifford 2002; Lal 2005; Poeplau and others 2011; Fuchs and others 2016). Changes in land use affect both the formation and the decomposition of SOC, which could turn soils into either a sink or a source of atmospheric CO_2 concentrations (Poeplau and others 2011; Hiltbrunner and others 2013; Bárcena and others 2014). The effects on the net C balance of soils, however, are often uncertain as our current knowledge is primarily based on case studies, and effect sizes and even directions depend on the type of LUC as well as on time (Poeplau and others 2011; Hiltbrunner and others 2013). Since the 1950s, European forest areas have expanded by over 25% (Janssens and others 2003; Kümmerle and others 2015), whereas cropland and grassland areas have steadily declined (Rounsevell and others 2003, 2006). In Central and South European mountainous areas, between 1990 and 2000 over 4% of agricultural land has been abandoned (Sjögersten and others 2011). In Switzerland, forest expansion has been the major land-use change with an areal increase of approximately 22% in the last century (Ginzler and others 2011). Currently, forests account for one-third of the country's area (Bolliger and others 2008; Brändli 2010). Similar to other Central-European countries, the largest forest expansion has occurred on marginal land in alpine regions, primarily at the expense of grassland (Gellrich and others 2007; Brändli 2010). In comparison with many other European regions, forests in Switzerland have primarily been managed as plenter forests with single-tree harvest and consequently a near-natural structure of forests (Angst 2012). Due to high costs of wood harvesting, the management intensity has even declined during the last decades (Brändli 2010). As a consequence, Swiss forests are characterized by a high mean tree age (more than ¼ of Swiss accessible forest area is older than 120 years, see Brändli and others 2015) and by the greatest stand biomass in Europe (Liski and others 2002). Forest expansion and development ultimately alters the climatic balance of terrestrial ecosystems including both radiative forcing via albedo changes and C sequestration. In these estimates, changes in SOC stocks represent the largest uncertainty (for Switzerland, see Schwaab and others 2015; for Europe: Fuchs and others 2016). Generally, forest soils contain high SOC stocks (Lal 2005) and thus, newly afforested soils are assumed to become a C sink due to reduced biomass removal, a larger rooting system with greater C input into the soil, and low litter quality (Lorenz and Lal 2010; Fuchs and others 2016). Deforestation and forest disturbance have frequently been observed to induce rapid SOC losses (Spielvogel and others 2006; Poeplau and others 2011; Achat and others 2015; Guillaume and others 2015), which in reverse suggests that forest expansion would lead to net soil C gains, but probably at a smaller rate (Jandl and others 2007). However, a number of recent case studies challenge this paradigm. Whereas an increase in SOC stocks is observed during cropland afforestation, the direction and magnitude of SOC storage is not as straightforward in the case of grassland afforestation. Hiltbrunner and others (2013), for example, found that afforestation of extensively grazed subalpine pasture had only a small effect on total SOC storage, with increasing stocks in the organic layer but decreasing SOC stocks in the mineral soil. Correspondingly, afforestation of abandoned subalpine grasslands in the Italian Alps decreased SOC stocks down to a soil depth of 30 cm (Guidi and others 2014), but in the German Alps the decline in the mineral soil was offset by a SOC accumulation in the organic layer (Thuille and Schulze 2006). Most studies only include surface soils when examining afforestation effects but C gains in surface soils are often offset by C losses in the subsoil (Vesterdal and others 2002, 2011; Poeplau and others 2011; Hiltbrunner and others 2013; Mobley and others 2015). Moreover, the type of the previous land use plays a crucial role for the afforestation effects with larger increases on former crop than on grassland (Poeplau and others 2011). In addition, SOC stock changes also depend on time since LUC has occurred, including a transition period following forest expansion, during which SOC stocks initially decrease and thereafter recover (Bárcena and others 2014). For example, case studies in the Netherlands indicate that organic layer only starts to accumulate 8 years after tree stands have been established (Vesterdal and others 2002) and converge to a higher ‘steadystate’ level after about 80–100 years (Böttcher and Springob 2001). Reflecting the observed patterns, soil C models suggest a sigmoidal increase of SOC stocks during forest development with a negligible initial increase of SOC stocks followed by high accumulation rates that eventually level out (Jandl and others 2007; Thürig and Kaufmann 2010). Thus, forest age is assumed to be crucial in predicting the time scales of the processes influencing SOC dynamics in forest soils. The magnitude and temporal dynamics, however, remain highly uncertain.

Historical land use has been recognized as relevant for current soil properties (Dupouey and others 2002; Gimmi and others 2013). Even though historical land-use practices have been shown to influence SOC stocks in the long-term (Schulp and Verburg 2009; Bárcena and others 2014), our quantitative knowledge is still limited due to the lack of historical soil samples and an uncertain land-use history. Most knowledge about afforestation effects on SOC stocks originates from a limited number of chronosequence studies (Bellemare and others 2002; Vesterdal and others 2002; Hiltbrunner and others 2013). An alternative approach is to assess the historical land use for a large number of sites and to estimate how current SOC stocks differ among soils with different land-use histories. For instance, Schulp and Verburg (2009) showed that historic land use (for example, forest degrading to heath) in the Netherlands is still imprinted in current SOC stocks. In contrast, historic forest management (for example, former selectively cut forests) was not reflected in current SOC stocks in the Hainich-Dün region in Germany (Wäldchen and others 2013).

In our study, we assessed the impact of ongoing forest expansion on SOC storage in Switzerland. Using historical and modern topographic maps, we reconstructed forest cover changes for the past 150 years and estimated the age of 857 current forest stands for which data on soil, vegetation and environment had been measured. Then, we examined the effect of forest age on current SOC stocks in the organic layer and mineral soil and compared it to other factors such as topography, climate, and soil properties. We expected that SOC stocks would increase with increasing forest age reflecting forest development but that the effect of forest age would be small as compared to the influence of forest type, climatic parameters and physico-chemical soil characteristics.

2. MATERIALS AND METHODS

2.1. Study Area and Sampling Sites

A total of 1047 soil profiles have been sampled across the entire forested territory of Switzerland (Figure 1). Switzerland can be categorized into five major biogeographic regions (Jura, Plateau, Pre-Alps, Alps, and Southern Alps) with specific climatic conditions, bedrock, and forest cover. The Jura, the Plateau, the Pre-Alps, and the northern part of the Alps are characterized by an oceanic and thus relatively humid climate, whereas the central part of the Alps has a continental climate. The Southern Alps have warm temperate so-called insubrian climate conditions (Gonseth and others 2001). The Jura is dominated by calcareous bedrock like limestone or marl, whereas the Southern Alps have mainly acidic bedrock such as granite or gneiss. The other regions have various types of bedrocks with the Plateau comprising mainly calcareous moraines or tertiary sediments (molasse), the Pre-Alps consisting mostly of calcareous sediments, and the Alps having very heterogeneous bedrocks (Gnägi and Labhart 2015). Forest covers almost half of the Jura (48%) and of the Southern Alps (47%), 25% of the Plateau, 33% of the Pre-Alps, and 22% of the area of the Alps region (Swiss National Forest Inventory, Brändli 2010). The fraction of conifer forest is greatest in the Alps (76%) and smallest in the Southern Alps (38%; Brändli 2010). The majority of our sampling sites are located on the Plateau (n = 277) and in the Pre-Alps (n = 260). The rest of the sites are distributed across the Alps (n = 176), Jura (n = 73), and the Southern Alps (n = 71). All sites are located in current forests with elevations ranging between 277 and 2207 m a.s.l..

2.2. Soil Data

The morphology of all soil profiles was determined and samples were collected by genetic horizons, down to 120 cm soil depth on average or to parent rock. Samples were dried at 40–60°C and sieved with a 2-mm mesh for chemical analysis. Soil pH was measured in 0.01 M $CaCl_2$. Basic cation contents (BC), comprising the sum of the exchangeable basic cations (Ca, Mg, K, and Na), was determined by extraction with unbuffered 1 M NH4Cl (soil/solution = 1:10, end-over-end shaker for 1 hour) and measured by an ICP-OES (Perkin Elmer Optima 7300DV) according to Walthert and others (2013). Humus forms were classified into: mull (only litter horizon present), moder (L + F horizon present), and mor (L, F, and H horizons present). Total and organic C contents were measured in ground samples by dry combustion using a C/N analyser NC 2500 (CE Instruments, Italy). Inorganic C in samples with a pH above 6.0 was removed with acid vapour prior to analysis (Walthert and others 2010). Mineral soil SOC stocks were calculated using the following equation:

$$SOC_{hz} = \sum_{i}^{z}(h_i\,(1 - \theta_i)\,\rho_i C_i\,) \qquad (1)$$

where SOC_{hz} is the SOC stocks of all horizons hz (kg C m^2), C_i is the carbon concentration of the horizon i (kg kg^{-1}), q_i is the density of the fine earth (g cm^{-3}), θ_i is the volumetric stone content (m^3 m^{-3}), and h_i is the horizon thickness (m). Fine earth density was estimated with a pedotransfer function, based on a calibration dataset of 559 mineral soil horizons from 134 different sites and a validation set of 131 horizons from 34 sites (see Nussbaum and others 2016 for details). The pedotransfer function relied on the SOC content, the square root of the sampling depth, the square root of the slope, the skeleton content, three field density estimates, and nine physiographical unit categories. The SOC stock in the organic layer was calculated according to Hagedorn and others (2010), where the mass of the organic layer was first calculated as a product of the density (L: 0.10 g cm^{-3}, F: 0.15 g cm^{-3}, H: 0.20 g cm^{-3}) and the volume (based on measured thicknesses), which was then multiplied with its C concentration. Finally, as soil profiles have been dug vertically, SOC stocks were corrected for the slope by multiplying them with the cosine of the slope. Carbon stocks were calculated for the organic layer (including L, F, and H horizons), for the mineral soil at 0–120 cm depth and for total carbon stocks equaling the sum of the two. Mean average contents of BC and pH were calculated for 0 to 30 and 0 to 120 cm depth intervals by weighting the averages of the contents with the amount of fine earth. Clay, silt, and sand contents of 600 sites were measured with the sedimentation method according to Gee and Bauder (1986). Field estimates, according to ten soil texture classes, were used for the rest of the samples (Walthert and others 2013). Soil type was classified according to the World Reference Base from 2007 (IUSS Working Group WRB 2007), and soil types were grouped into calcareous, acidic, and waterlogged soil groups.

Calcareous and acidic soils were separated by setting the lime limit to one meter soil depth, while the waterlogged soils comprised Gleysols and Stagnosols. Rooting depth was assessed directly in the soil pits.

2.3. Relief, Climatic, and Vegetation Data

Altitude and slope were determined from a 25-m digital elevation model (DEM, Swisstopo 2011). Climate data were based on the Swiss meteorological network MeteoSwiss combined with suitable interpolation methods. Mean annual precipitation (MAP) and temperature (MAT) for the period 1981–2010 were provided by Meteotest (see Remund and others 2014 for details). Plant species in herb, shrub, and tree layers were determined using the Braun-Blanquet cover abundance scale (Braun-Blanquet 1964). The broadleaf percentage was calculated as the sum of the cover of all broadleaf species divided by the sum of the cover of all tree species at canopy level. Using this percentage, forest type was subdivided into two classes: coniferous (0–50%) and broadleaf (51–100%) forests. Exposition and relief were measured directly at the soil pit according to their position in the field (for example, North-West for exposition and hilltop for relief).

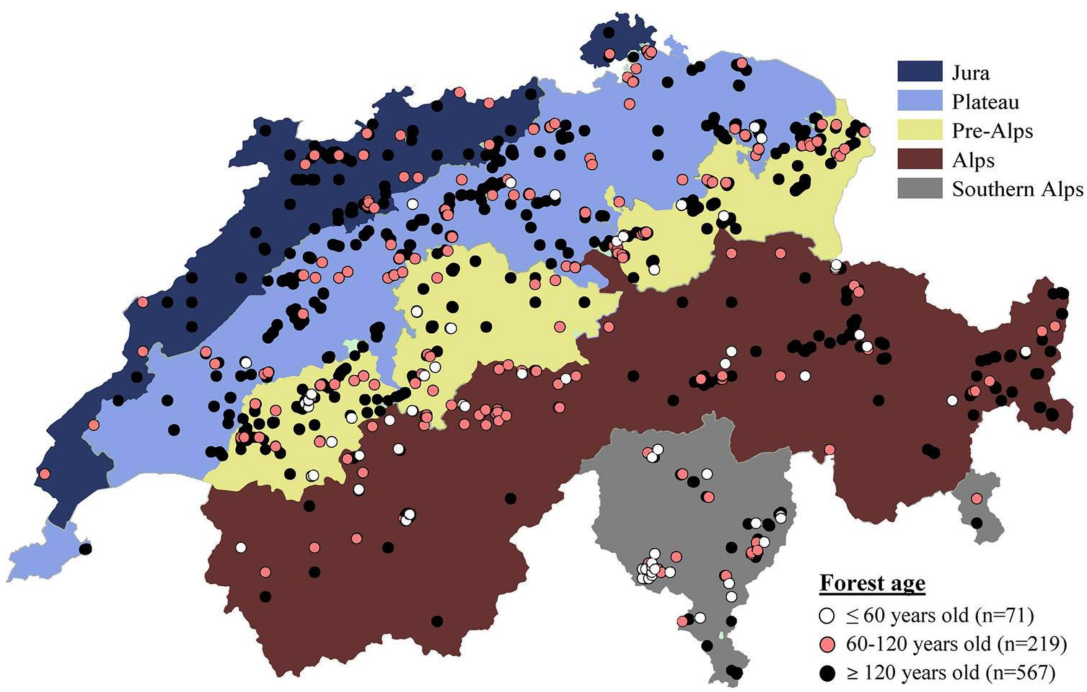

Figure 1. Map of Switzerland showing the distribution of the forest soil sites (n = 857) according to forest age classes.

2.4. Reconstruction of Past Forest Cover Change

Historic forest cover change at the 1042 sampling sites was determined by analyzing historical and modern topographic maps across Switzerland at eight time periods. The oldest map showing forest cover for Switzerland is the so-called Dufour original survey map which dates back to 1850 (Figure 2A, D). This map has a scale of 1:25000 in the Swiss Plateau and Jura and 1:50000 in Alpine regions. For the 1900–1950 period, Siegfried maps, with the same scale as the Dufour maps, were used (Figure 2B, E). For 1950–2011, modern topographic maps were available (Figure 2C, F, Swisstopo 2011). All maps were available in digitized and geo-referenced form; spatial accuracy of the digitized maps was evaluated by comparing intersection of coordinate lines with modern topographic maps (Ginzler and others 2011). Because each map set was generated over a period of 10–20 years, we examined forest cover changes not for single years but for time periods (1850, 1880–1900, 1910–1920, 1920–1930, 1952–1970, 1970–1990, 1990–2011, 2011). Forest cover was classified into four categories: forest, open forest, forest edge, and non-forest. The distinction between closed forest, forest edge, and an open forest was done based on the distance of a site to the mapped forest edge. A site was classified as a closed forest site if it was located at least 25 m from the mapped forest edge (inside buffer). A non-forest site was defined as a site at least 50 m from the mapped forest edge (outside buffer). A site was classified as forest edge when it was ± 25m from the mapped forest edge (inside and outside buffer). Finally, a site was classified as open forest when the map showed a tree canopy that did not form a continuous closed cover. Some maps covering the 1850–1900 periods had missing map parts. As a result, it was impossible to identify forest cover for 89 sites, which were removed from further analysis. Five sites, classified as Histosols, were excluded from the analysis due to their extraordinary properties. Only the sites classified as forest sites in 2011 were considered in the estimation of the forest age. Furthermore, sites were only included in the analysis if there were no interruptions in the forest cover for more than 20 years. Overall, our analysis allowed the estimation of the minimal forest age for 857 currently closed forested sites. The forest sites were subdivided into three time periods of minimal forest ages—sites of at least 120 years of age (here referred to as 'old forest sites') as well as two younger forest site groups, including sites of forest age between 60 and 120 years (here referred to as 'medium') and sites younger than 60 years (here referred to as the 'young'). All map evaluations were completed with ArcGIS 10.1 software.

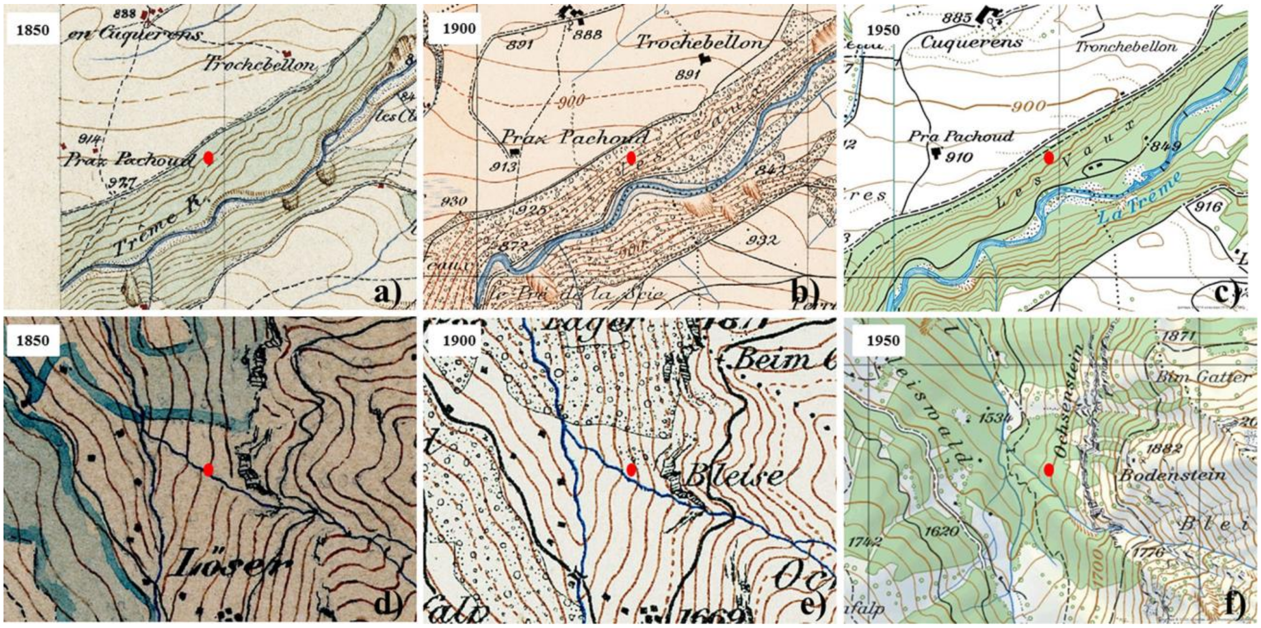

Figure 2. Examples of historical land-use change of soil sites in old forest with a permanent forest cover (A, B, C) and in a newly afforested (D, E, F) forests.

2.5. Statistical Analysis

Analysis of variance (ANOVA) tests after variable selection were used to detect if forest age affects SOC stocks as well as to identify the variables with the strongest effect on SOC stocks. All statistical tests were performed in the statistical software R 3.0.3 (R Core Team 2015; Harrell and Others 2015; Heiberger 2015; Neuwirth 2014, Ripley 2015; Venables and Ripley 2002; Lemon 2006; Wickham 2007, 2009, 2011, 2015; Wickham and Francois 2015). For the variable selection, SOC stocks and the other variables were fed into a regression tree model (R package 'tree') to define which were important determiners of SOC stocks (Crawley 2007). The following variables were fed into tree models: altitude, forest type, root depth, soil group, topography (exposition, relief, slope), climate (MAP and MAT), soil texture (clay, silt, sand contents), soil chemistry (pH and BC contents). The variables, selected by the tree model as most appropriate, were then included in an ANOVA model. In addition to the tree regression model selection, we identified inter-correlated variables and excluded the ones with the weaker explanatory power to prevent further correlations. The following variables were excluded from further analysis: for organic layer, mineral soil, and total SOC stocks—root depth, slope, clay, and silt contents; for organic layer—MAP, slope, sand contents, altitude, relief; for mineral soil—MAT and relief; for total SOC stocks—altitude, MAT, and sand content. To determine the order in which the variables were fed into the ANOVA model, simple regressions were used to detect whether the variables correlate with forest age. The ones correlating with age were fed after forest age in the model and the ones not correlated— before forest age. In the ANOVA, we used the function Aov.ko with a keep.order option set true to prevent reordering of independent variables in the model. The ANOVA models were checked for multicollinearity using the variance inflation function (VIF, R-package 'HH'), setting the value of 5 as a threshold for evidence of multicollinearity. Tests were performed for SOC stocks in the organic layer and the mineral soil, as well as for total SOC stocks. Models were manually fitted to the minimum adequate model until all terms in the model were significant. As a post-hoc test, the Tukey's HSD test was performed to determine which of the forest age classes differ significantly from each other. In order to avoid confounding effects by waterlogged soils with very high SOC stocks, we analyzed the dataset twice, once including and once excluding them (n = 125). In addition to forest age, sites were examined according to forest type, regardless if this occurred in the tree model or not (which it did in the organic layer and total SOC stocks but not in the mineral soil). Furthermore, interactions were included in the tests (forest age x soil group, region x soil group, soil group x BC, pH x forest type). Due to the non-normality of our dataset, SOC stocks were log-transformed to approximate normality. The normality of the residuals was tested using histograms and Shapiro-Wilk Normality test. The data in the manuscript is presented as means ± standard error. Effects with $P < 0.05$ are considered statistically significant, while P values < 0.1 are considered marginally significant.

3. RESULTS

3.1. Site and Soil Characteristics

The soil sampling sites in current Swiss forests have a MAT ranging from 0.6 to 11.9°C and a MAP from 705 to 2340 mm. Predominant soil types were Cambisols (n = 320), Luvisols (n = 115), and Gleysols (n = 80); soils groups were almost equally distributed between calcareous (n = 390) and acidic (n = 324) sites, whereas waterlogged (n = 125) were the smallest group. There were 415 sites covered by broadleaf trees, 422 coniferous sites, and 20 sites, where information on tree species was not available. The pH values of soil depth 0–30 cm ranged between 2.8 and 7.8, and at a depth of 0–120 cm, it ranged between 2.8 and 7.9.

3.2. Reconstruction of Forest Cover

The reconstruction of the past forest cover of currently forested sites using historical maps showed distinct changes in the distribution of closed and open forests, forest edges, and non-forested land (Figure 3). In the first mapping year in 1850, 157 of the 958 sampled sites have been non-forested, whereas this number has drastically decreased 100 years later, with most of these sites transitioning to closed forest. Changes in sites at the forest edge decreased from 120 in 1850 to 90 in 2011, whereas open forest sites were always less than 20. For the estimation of the minimal forest age, only sites located in currently closed forest areas were considered (n = 857; Figure 3). This rather strict site selection helped to prevent inclusion of ambiguous sites, such as sites with a short discontinuity in forest cover. The analysis of minimal forest ages indicated that 71 sites belonged to the group of forest sites younger than 60 years, 219 to the sites between 60 and 120 years, and finally 567 were identified as old forest sites with a forest age of at least 120 years.

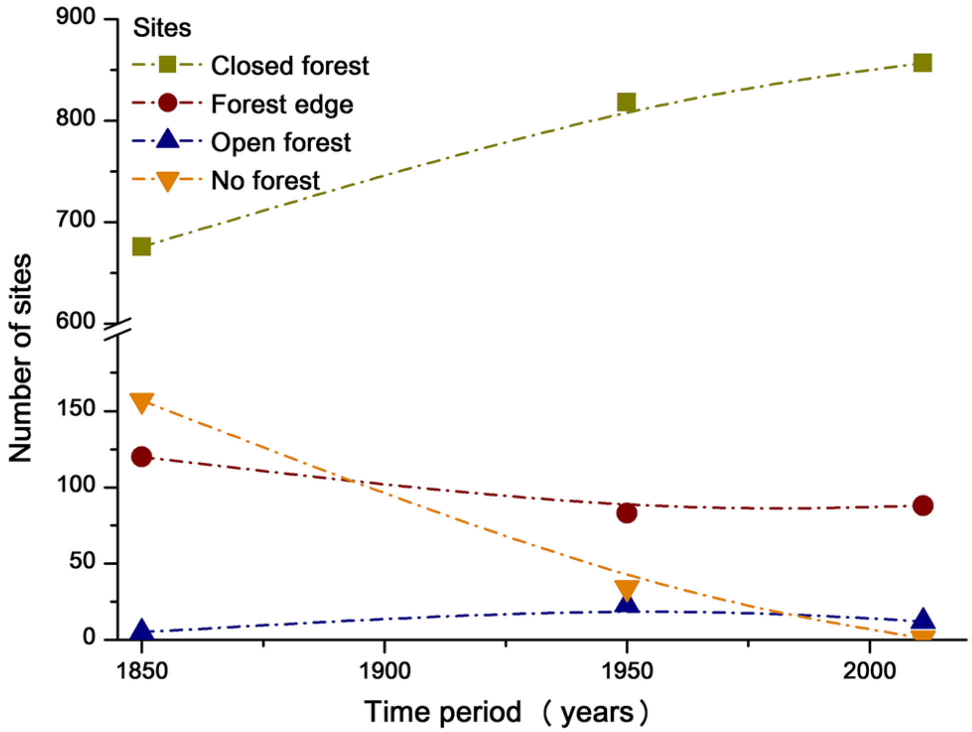

Figure 3. Forest cover change of the sites throughout the years. Distinction between closed forest, forest edge, and open forest depends on the distance of a site to the mapped forest edge. The sites currently located in closed forest areas (n = 857) were used for estimating the minimal forest ages.

Among the five biogeographic regions, the highest fractions of permanently forested sites were found in the Jura and Swiss Plateau, in particular in the Bernese lowlands (see Figure 1). The highest fraction of young forest sites was observed in mountainous regions, particularly in the Alps and Southern Switzerland. Environmental conditions potentially influencing SOC stocks varied among the forest age classes. On average, newly afforested sites were located at higher altitudes compared to old forest sites (1089 ± 50.3 vs. 854 ± 16 m a.s.l.) and they had a corresponding slightly lower MAT and higher MAP (Table 1). Furthermore, young sites had slightly lower clay contents compared to old ones. Both younger site classes had a higher cover with coniferous (55%) than with broadleaf trees compared to the old forested sites (48%). Other properties (for example, pH) did not differ significantly among the forest age classes.

3.3. SOC Stocks in the Organic Layer

The majority of the soils had a mull-type organic layer (n = 489), followed by moder (n=231), mor (n=119), and other less abundant organic layers such as Tangel (n=5) and peat (n=2). At 11 sites, organic layers have not been classified. Organic layers had mean SOC stocks of 2.4 kg C m^{-2} and a median of 0.9 kg C m^{-2}. Sites in the medium category contained the highest SOC stocks (3.0±0.3 kg C m^{-2}) compared to the young sites (2.7±0.4 kg C m^{-2}) and the old ones (2.2±0.2 kg C m^{-2}).

Table 1: Cross-comparison of basic environmental variables between different forest age categories.

Parameters	< 60	60-120	> 120	Forest age comparison	p adj
Base Cations (at 30cm soil depth, in mmcolc/kg)	100.1±13.5	135.2±10.7	134.8±6.1	Medium - Young Old - Young Old - Medium	n. s. n. s. n. s.
pH (at 30cm soil depth)	4.8±0.2	4.9±0.1	5.0±0.1	Medium - Young Old - Young Old - Medium	n. s. n. s. n. s.
Clay content (at 30cm soil depth, in %)	17.8±1.2	20.5±0.8	21.8±0.5	Medium - Young Old - Young Old - Medium	n. s. 0.02 n. s.
Altitude (m a. s. l.)	1089.0±50.3	1000.2±28.3	854.3±16	Medium - Young Old - Young Old - Medium	n. s. < 0.05 < 0.05
Slope (%)	50.2±2.9	41.3±2	35.1±1.2	Medium - Young Old - Young Old - Medium	0.05 < 0.05 0.02
MAT (°C)	6.8±0.3	7.1±0.1	7.6±0.1	Medium - Young Old - Young Old - Medium	n. s. < 0.05 < 0.05
MAP (mm)	1540.4±42.3	1388.1±23.2	1330.3±12.7	Medium - Young Old - Young Old - Medium	< 0.05 < 0.05 0.07
P-values are based on TukeyHSD Anovas, where the means of the forest age categories are compared according to the variables at a confidence level of 0.95.					

A combination of tree models and expert knowledge was used to identify the most appropriate parameters for the ANOVA model. The final set of parameters included pH and BC (mean values at 0–30 cm soil depth, see Table 2), MAT, soil group, forest type, and region, as well as, the following interactions: region x soil group, soil group x BC, soil group x forest age, and pH x forest type. During the manual fit of the model, the interaction soil type x forest age was removed due to insignificance and the interaction region x soil group due to evidence of multicollinearity. In the final ANOVA model, BC and soil group had the strongest effect on SOC stocks in the organic layer, with the highest SOC stocks in acidic soils, for example, Podzols and Planosols (average pH of 3.6 for both soil types). Accordingly, pH had a strong effect, with SOC stocks in the organic layer decreasing with increasing pH. Forest type had also an impact on SOC stocks with conifer sites containing higher SOC stocks in the organic layer than broadleaf sites (3.8 vs. 1.0 kg C m^{-2}), regardless of forest age (Figure 4). Additionally, organic layer SOC stocks decreased significantly with increasing MAT (Figure 5). The regional distribution showed a significant impact as well, with highest SOC stocks found in the alpine regions (see Electronic supplementary material). The overall model explained 43% of the variance (adjusted R2; Table 2). Forest age only had a marginally significant impact ($P = 0.06$, SS = 0.4%, see Table 2). Excluding waterlogged soils from the analysis increased the significance of forest age slightly, but the effect remained weak ($P = 0.03$, SS = 0.6%). The post hoc TukeyHSD test showed a significant difference in mean SOC stocks between medium forests with a 55% cover of conifers and old forests with a 48% conifer cover (P adj. = 0.04 and P adj. = 0.03, with and without waterlogged soils, respectively). In the analysis of the individual biogeographic regions in Switzerland, forest age did not significantly affect SOC stocks in the organic layer in any of the regions (see Electronic supplementary material). The effects of forest type, pH, and soil group prevailed in most regions (for example, soil group explained almost 20% of the model variance in Jura), demonstrating that SOC stocks in the organic layer are influenced primarily by soil chemistry and forest type. MAT was an important explanatory variable for all regions but Jura. For instance, in the region of the Southern Alps, MAT explained 23% of the variance.

3.4. SOC Stocks in the Mineral Soil (0–120 cm Soil Depth)

Carbon stocks in the mineral soil (down to a depth of 120 cm) showed an overall mean of 10.9 kg C m^{-2} and a median of 9.2 kg C m^{-2}. Based on the tree model, soil group, MAP, BC, and sand content (mean values at 0–120 cm soil depth), as well as slope, altitude, and exposition, were fed into the ANOVA model. In addition, forest age, forest type, region, as well as, the interactions: region x soil group, soil group x forest age, and soil group x BC were added to the model as well. MAP had a strong positive effect on SOC storage ($P < 0.05$, Figure 6), explaining a large part of the model variance (sum of squares (SS) = 8.3%, Table 2). In addition, soil group was highly significant ($P < 0.05$), with the highest SOC stocks in waterlogged soils. Moreover, there was a negative relationship with slope and sand content and the interaction soil group x BC was the only interaction to have a significant impact on SOC stocks. Forest age showed a significant impact on SOC stocks ($P < 0.05$); however, its explanatory power (SS = 0.8%) was the lowest of all variates. The interaction forest age x soil group was removed from the model during fitting due to insignificance. Interestingly, the highest SOC stocks were found in the young forest sites (12.5 ± 0.9 kg C m^{-2}, Figure 4) and the lowest ones in old forests (10.5 ± 0.3 kg C m^{-2}). The model explained 32% of the variance. When waterlogged soils were excluded, forest age was also found to be significant and had a slightly higher explanatory power (SS = 1.7%). However, the effect was considerably smaller compared to other variables. Calcareous and acidic soils had identical SOC stocks in the mineral soil (10.3 kg C m^{-2}; n. s.). The ANOVA model explained almost 31% of the variability. The post hoc TukeyHSD test showed significant differences between the means of the old and medium (P adj. < 0.05) as well as between old and the young (P adj. < 0.05) forest age categories. Among the biogeographical regions, the Southern Alps contained the highest SOC stocks with 15.8, 16.9, and 14.1 kg C m^{-2} for the young, mid-age, and old forest sites, respectively (Electronic supplementary material). Only the medium forests in Jura had similarly high SOC stocks of 17.1 kg C m^{-2} in the young forests. Forest age had a marginal significant impact on SOC stocks only in the Alps region, whereas the interaction soil group x forest age was significant in the Swiss Plateau. However, soil group and BC exerted stronger effects in all regions. MAP influenced SOC stocks in all regions except the Jura, whereas forest type and slope were important explanatory variables for the Jura and the Pre-Alps.

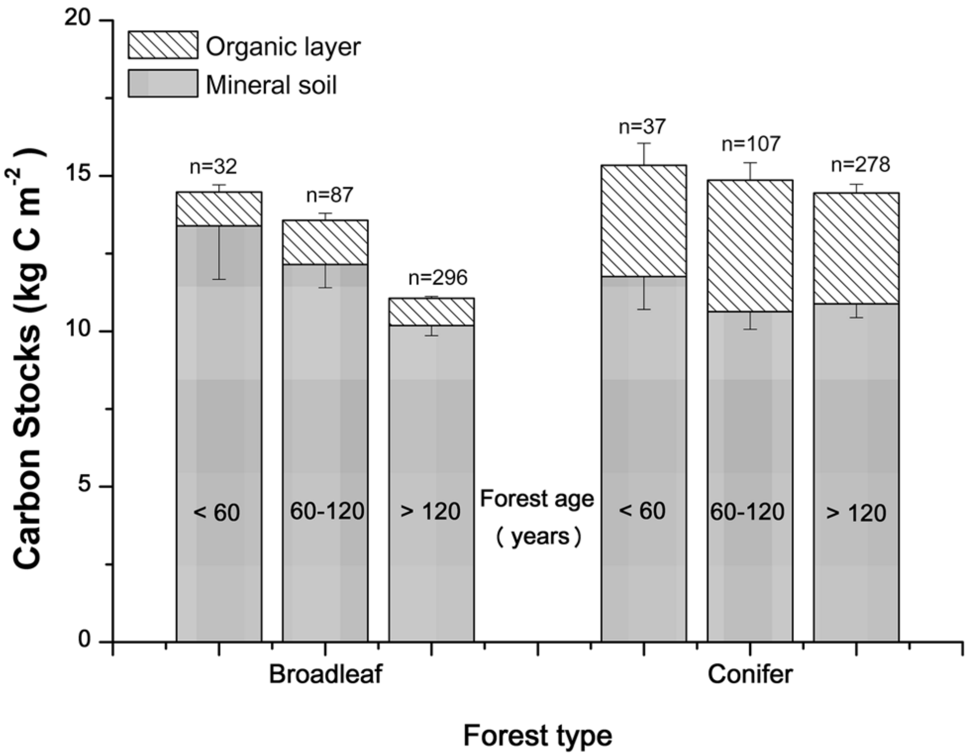

Figure 4. Effects of forest type (broadleaf and conifer) for the three forest age categories on SOC stocks in the organic layer and mineral soil at 0–120 cm soil depth. Error bars represent standard errors.

Table 2: Effect of forest age and other variables on SOC stocks.

Parameter	Df	SS (%)	F	Parameter	Df	SS (%)	F	Parameter	Df	SS (%)	F
Including waterlogged soils											
Organic layer				***Mineral Soil***				***Total C stocks***			
Region	4	5.8	$F_{(4,821)}$ = 21.413 ***	**Region**	4	8.4	$F_{(4, 829)}$ = 25.666 ***	**Region**	4	5.7	$F_{(4, 816)}$ = 17.230 ***

Soil group	2	8.8	$F_{(2,821)}$ = 64.781 ***	**Soil group**	2	3.2	$F_{(2, 829)}$ = 19.640 ***	**Soil group**	2	2.5	$F_{(2, 816)}$ = 14.917 ***
BC	1	9.6	$F_{(1,821)}$ = 140.644 ***	**Forest age**	2	0.8	$F_{(2, 829)}$ = 5.059 **	**Forest age**	2	1.1	$F_{(2, 816)}$ = 6.411 **
Forest age	2	0.4	$F_{(2,821)}$ = 2.788 .	**MAP**	1	8.3	$F_{(1, 829)}$ = 101.112 ***	**BC**	1	3.1	$F_{(1, 816)}$ = 37.892 ***
MAT	1	3.6	$F_{(1,821)}$ = 52.731 ***	**Slope**	1	3.0	$F_{(1, 829)}$ = 36.953 ***	**Relief**	4	1.2	$F_{(4, 816)}$ = 3.608 **
pH	1	7.0	$F_{(1,821)}$ = 102.572 ***	**Sand content**	1	2.2	$F_{(1, 829)}$ = 26.400 ***	**Forest type**	1	5.0	$F_{(1, 816)}$ = 61.490 ***
Forest type	1	2.6	$F_{(1,821)}$ = 37.920 ***	**Soil group x BC**	3	6.0	$F_{(1, 829)}$ = 24.493 ***	**Slope**	1	5.9	$F_{(1, 816)}$ = 71.865 ***
Soil group x BC	2	4.8	$F_{(2,821)}$ = 35.333 ***	**-**	-	-	-	**MAP**	1	7.8	$F_{(1, 816)}$ = 94.602 ***
pH x forest type	1	1.5	$F_{(1,821)}$ = 21.727 ***	**-**	-	-	-	**Soil group x BC**	2	0.6	$F_{(2, 816)}$ = 3.817 *
Residuals	821	55.9	-	**Residuals**	829	68.0	-	**Residuals**	816	67.1	-
Excluding waterlogged soils											
Organic layer				***Mineral Soil***				***Total C stocks***			
Region	4	6.1	$F_{(4, 699)}$ = 17.560 ***	**Region**	4	10.9	$F_{(4, 702)}$ = 27.960 ***	**Region**	4	7.7	$F_{(4, 693)}$ = 20.125 ***
Soil group	1	6.5	$F_{(1, 699)}$ = 74.302 ***	**Forest age**	2	1.7	$F_{(2, 702)}$ = 8.650 ***	**Soil group**	1	0.6	$F_{(1, 693)}$ = 6.299 *
BC	1	6.7	$F_{(1, 699)}$ = 76.596 ***	**MAP**	1	7.9	$F_{(1, 702)}$ = 80.679 ***	**Forest age**	2	2.0	$F_{(2, 693)}$ = 10.605 ***
Forest age	2	0.6	$F_{(2, 699)}$ = 3.533 *	**Slope**	1	2.9	$F_{(1, 702)}$ = 29.166 ***	**BC**	1	2.1	$F_{(1, 693)}$ = 22.062 ***
MAT	1	3.6	$F_{(1, 699)}$ = 41.000 ***	**Sand content**	1	2.3	$F_{(1, 702)}$ = 24.002 ***	**Relief**	4	1.8	$F_{(4, 693)}$ = 4.598 **
pH	1	7.9	$F_{(1, 699)}$ = 90.671 ***	**Region x Soil group**	5	1.7	$F_{(5, 702)}$ = 3.384 **	**Forest type**	1	4.8	$F_{(1, 693)}$ = 49.890 ***
Forest type	1	2.9	$F_{(1, 699)}$ = 33.499 ***	**Soil group x BC**	2	3.9	$F_{(2, 702)}$ = 20.037 ***	**Slope**	1	6.2	$F_{(1, 693)}$ = 64.671 ***
Soil group x BC	2	4.9	$F_{(1, 699)}$ = 57.080 ***	-	-	-	-	**MAP**	1	7.5	$F_{(1, 693)}$ = 77.883 ***
-	-	-	-	-	-	-	-	**Soil group x BC**	1	0.7	$F_{(1, 693)}$ = 6.856 **
Residuals	699	60.8	-	**Residuals**	702	68.7	-	**Residuals**	693	66.6	-

The abbreviation *df* stands for degrees of freedom, *SS* represents the sum of squares in %, *F* represents the F-value. The annotation (“-”) means that the variable was not present in the final model fit.

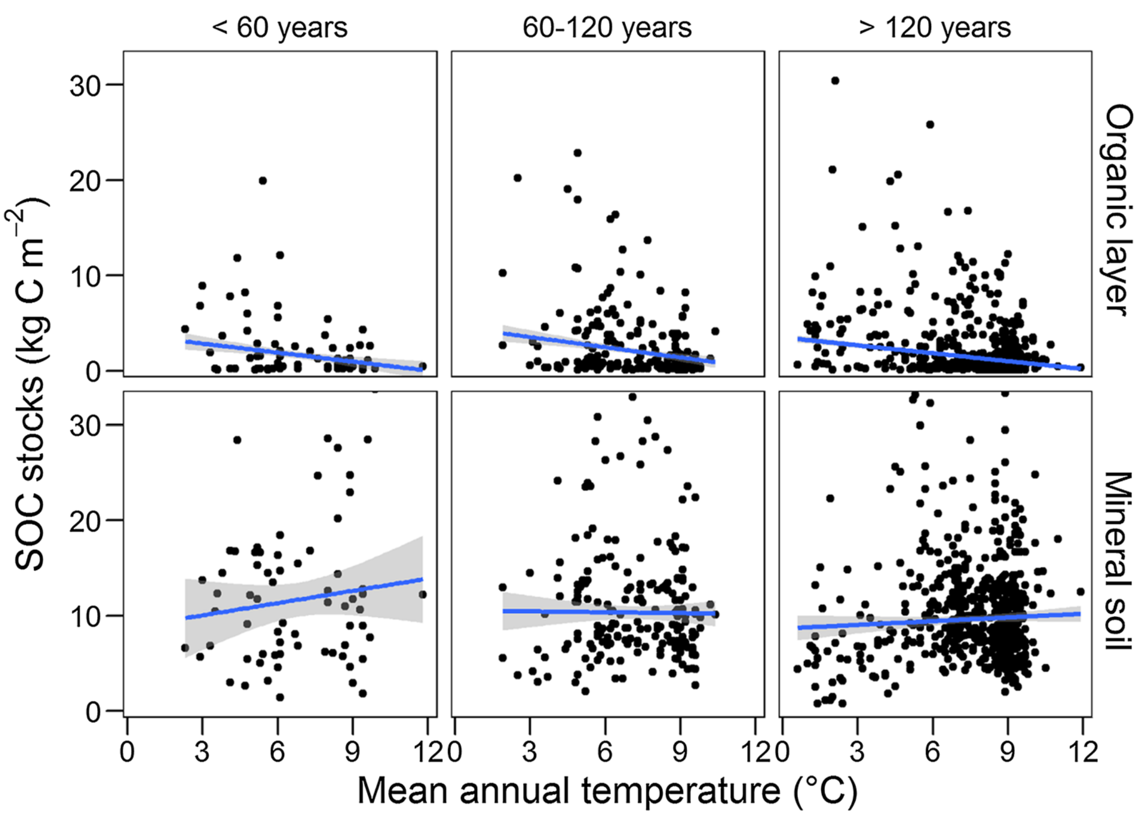

Figure 5. Relationship between SOC stocks (kg C m^{-2}) in the organic layer and the mineral soil (0–120cm) and MAT (°C) for the different forest age categories. Lines represent robust linear regression, areas delineating the lines represent confidence intervals.

A separate analysis of soil data at 0–30 cm depth showed an almost identical result with forest age not significant and MAP, BC and slope having the strongest effects on SOC stocks (data not shown).

3.5. Total SOC Stocks

Total SOC stocks had an overall mean of 13.3 kg C m^{-2} and a median of 11.6 kg C m^{-2} (data not shown). Based on the tree model, we used the following variables in the ANOVA model: MAT, BC, MAP, slope, soil group, relief as well as the interactions region x soil group, soil group x BC, and soil group x forest age in addition to forest age, forest type, and region. The model explained 33% of the overall variance. The strongest impact was exerted by MAP, followed by slope, region, and forest type (Table 2). SOC stocks were positively related to MAP, whereas SOC stocks decreased with increasing slope. Relief was found to also have an impact, with the highest SOC stocks found at foothills. Furthermore, soil group had a significant impact (Figure 7) as well as BC and the interaction soil group x BC, suggesting that SOC stocks are influenced by the chemical composition of soils. Finally, there was a significant effect of forest type on total SOC stocks, with higher SOC stocks under conifer forests.

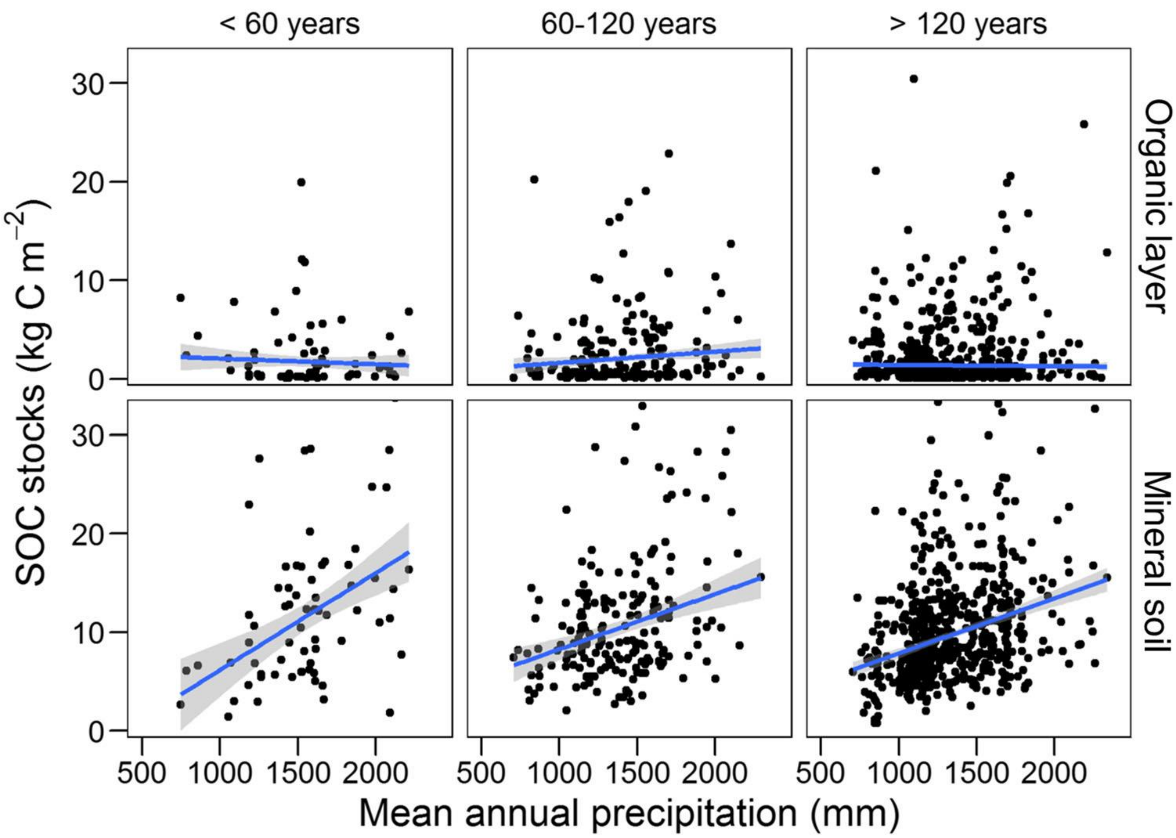

Figure 6. Relationship between SOC stocks in the organic layer and the mineral soil (0–120 cm soil depth) and MAP (mm) for the different forest age categories. Lines represent robust linear regression, areas delineating the lines represent confidence intervals.

Forest age had a significant impact on total SOC stocks ($P < 0.05$), with old forest sites containing the smallest SOC stocks (12.7 ± 0.3 kg C m^{-2}), compared to medium (14.3 ± 0.5 kg C m^{-2}) and young ones (14.9 ± 1 kg C m^{-2}). However, compared to the other variables in the ANOVA, forest age explained only a very small percentage of the model variance (SS = 1.1%). The TukeyHSD test indicated significant differences in the means between old and medium sites (P adj. = 0.02) and between old and young (P adj. = 0.05), but not between the two younger forest groups (P adj. = 0.983). The analysis was additionally performed excluding waterlogged soils, which resulted in a weaker effect of soil group, indicating that total SOC stocks did not differ significantly between acidic and carbonate bedrock. Even though the effect of forest age was more significant ($P < 0.05$) and had a higher explanatory power than with waterlogged soils (SS = 2.0%), the influence of other variables was still stronger (Table 2). A further separation of the young forests into age classes showed average SOC stocks of 16.3 ± 1.8 kg C m^{-2} for the less-than-20-year-old forest, 14.4 ± 1.3 kg C m^{-2} for the 20–40-year old, and 12.8 ± 2.2 kg C m^{-2}

for the 40–60-year old forests (see Electronic supplementary material). Hence, also within the young forests, SOC stocks decreased, but too few sites prevented an ANOVA.

3.6. Forest Edge Sites

An additional analysis of forest edges sites (within 25 m distance from a forest edge) with a consistent forest cover history (n = 76) showed that these sites had similar SOC stocks as the closed forest with a mean stock of 2.9 kg C m^{-2} in the organic layer and 11.1 kg C m^{-2} in the mineral soil (0–120 cm). In agreement with the closed forest, soil chemical variables (pH and BC) had the strongest effect on SOC stocks in the forest edges, whereas forest age was not significant (data not shown).

4. DISCUSSION

Our evaluation of historical forest cover for 857 currently forested soil sites revealed that forest age representing forest development on formerly non-forested land had only small effects on SOC stocks in Swiss forest soils with slightly smaller SOC stocks in old than in young forests. In comparison, other factors such as climate and soil chemistry were found to exert a much stronger influence on SOC stocks. The observed small and even negative changes in SOC stocks with forest age challenge the paradigm that mature forests contain the greatest SOC stocks (Lal 2005) and that SOC increases during forest development even several decades after land-use changes (Lettens and others 2004). However, our analysis, based on historical maps, could be biased by significantly different environmental site conditions in the forests of different ages. The comparison of potential drivers for SOC storage revealed that new forest sites were located on average 200 m in altitude higher than the old ones and at steeper slopes, reflecting that forest expansion due to land abandonment during the last decades has been more pronounced in mountainous regions, while the distribution of land cover types has changed less under more favorable warmer climatic conditions (Gellrich and others 2007; Brändli 2010). Due to the higher elevation, new forest sites had slightly lower mean annual temperatures (-0.8°C difference on average) and higher mean annual precipitation (+210 mm difference on average) as compared to the older ones. In comparison, soil properties (pH, soil texture, BC) hardly differed among the forest age categories. Therefore, we assume that our countrywide soil survey using historic maps is largely representative for a chronosequence of forest expansion and development. Applying the observed linear positive relationship between SOC stocks and MAP (+0.0081 kg SOC m^{-2} per mm; R^2 = 0.12***; Figure 6) suggests that the young sites had approximately 1.2–1.7 kg C m^{-2} greater inherent SOC stocks than medium and old forested sites. This estimate is similar to the observed difference of 0.6 and 2.2 kg C m^{-2} between the different forest age categories. We therefore conclude that the ‘unbiased’ forest age effect is rather small, especially as compared to the C accumulation in forest biomass. For instance, along an afforestation chronosequence in a subalpine grassland, biomass C has accumulated 42 kg C m^{-2} during a period of 120 years (Hiltbrunner and others 2013). Furthermore, the Swiss national forest inventory indicates an increase in forest biomass C due to the ongoing forest expansion and a greater forest growth as compared to wood harvest by almost 0.35 kg C m^{-2} from 1995 until 2005 (Brändli 2010). This comparison indicates that SOC losses with forest development of less than 1 kg C m^{-2} observed here on a centennial time scale are at least an order of magnitude smaller compared to C gains by an increase in forest biomass. In our assessment, we cannot rule out that SOC stocks might have increased during the first decades after forest expansion. However, chronosequence studies rather indicate SOC stocks to decrease initially following afforestation, particularly in the mineral soil (Poeplau and others 2011; Hiltbrunner and others 2013).

To our knowledge, there exists no study with information on historical forest cover and similar site conditions. However, our conclusion that forest age had a small effect on total SOC stocks is corroborated by the results of Wiesmeier and others (2013) in Bavaria (Germany), who found that land use (forest, grassland, cropland) had a smaller impact on SOC stocks as compared to soil type and climate. For the Bavarian Alps, Prietzel and others (2016) even concluded that climatic warming has induced SOC stock losses. Furthermore, Thuille and Schulze (2006) found only negligible effect of afforestation on SOC storage in the Italian Alps, but higher SOC stocks in sites with high precipitation. Our and the other studies are in contrast to the study by Schulp and Verburg (2009) in the Netherlands, where historical LUC was found to explain SOC variability better compared to present LUC. Their results, however, are based on four small-scale regions, with a historic transition from open forests and heathlands to agricultural systems on sand areas with Plaggen soil, causing a large additional input of organic matter. One reason for the apparently small and slightly negative effect of forest cover age on SOC stocks could be litter raking in Swiss forests for several centuries until the early 20th century, which substantially reduced C inputs into soils of the old forest (Gimmi and others 2013) preventing a SOC accumulation during stand development. Since clear-cutting is not allowed in Switzerland and forest have traditionally been managed as planter forests (Angst 2012), it seems unlikely that other more severe management practices have reduced SOC storage in old forests as it has been observed in Finland (Peltoniemi and others 2004). The most likely explanation for the negligible effect of forest cover age on SOC stocks is the dominant historic land use of the newly afforested sites in Switzerland as grasslands, which generally have similar SOC stocks as forests (Poeplau and others 2011). Unfortunately, historical maps do not provide information on the type of previous land use. In their analysis of natural forest regrowth, Gellrich and others (2007) observed that reforestation in Switzerland during a decade between 1980s and 1990s has mostly been taking place on former alpine pastures and grasslands in mountainous regions. Moreover, 85% of the current agricultural lands above 600 m a.s.l. are used as grasslands (FOEN 2012) and only 18% of our young forest sites are below this altitude. We therefore assume that the majority of our young forest sites had once been alpine pastures and marginal grasslands. This assumption is also supported by the fact that afforestation in Europe has taken place to a large extent (73% of all afforested lands) on former extensively used grasslands (Vesterdal and others 2011). Although afforestation can strongly affect the microclimate as well as the amounts and quality of litter inputs (Hiltbrunner and others 2013), a number of case studies indicate that the change from grasslands to forests has rather small effects on total SOC stocks. For example, a European-wide land-use change study by Poeplau and Don (2013) observed an impact on SOC stocks for all examined land-use changes except for afforestation on grassland. Two other chronosequence studies in temperate mountainous regions by Thuille and Schulze (2006) and Guidi and others (2014) reported SOC stocks in the mineral soil to even decrease after grassland afforestation. Also the meta-analysis of case studies by Poeplau and others (2011) observed a slight decrease in SOC stocks after grassland afforestation. Thus, if we consider the site conditions in our historical map-based study, we are confident that the negligible and rather negative change in SOC stocks with increasing forest age is robust. In contrast to our hypothesis that particularly in the organic layer, older forests would have higher SOC stocks we did not observe a consistent pattern. The highest SOC stocks in the organic layer were found in the medium 60- to 120-year-old forests. This pattern is in contradiction to chronosequence studies showing that organic layers are accumulating C with time following forest expansion, reaching a new equilibrium after 10 to 80 years (Böttcher and Springob 2001; Paul and others 2002; Vesterdal and others 2002; Hiltbrunner and others 2013). The inconsistent pattern in the organic layer can be attributed to the dominance of thin mull-type organic layers, which are biologically very active and reach an equilibrium more rapidly (<60 years) compared to thick mor-type organic layers, where organic matter accumulates at a slower rate. Furthermore, the majority of the medium sites were found in the Pre-Alps and the Alps, areas with relatively thick and SOC-rich organic layers (see Electronic supplementary material). Moreover, the old age group had the lowest contribution of coniferous trees (48%) as compared to the two younger ones (55%) and SOC stocks under coniferous forests contained on average 2.8 kg C m^{-2} higher SOC stocks in the organic layer than under broadleaf forests. However, even when we only included coniferous forests in our analysis, there was no consistent effect of forest age. Our findings of a dominant influence of tree species on SOC storage in the organic layer are supported by the afforestation study by Vesterdal and others (2002), who observed a three times greater increase in SOC stocks during afforestation with spruce than with oak. Furthermore, the study on past forest management by Wäldchen and others (2013) concluded that SOC stocks are affected by tree species but not by past forest management. Therefore, the selection and promotion of tree species would be a potential management practice to increase SOC storage in forests (Vesterdal and others 2013; Wiesmeier and others 2013).

In our study, other factors such as climate, soil group and soil chemistry exerted a much stronger effect on SOC stocks than forest age. Our conclusion is confirmed by the studies in Bavaria by Wiesmeier and others (2012, 2014), observing soil type to have a dominant influence on SOC storage. In Switzerland, there are particularly high SOC stocks in the acidic 'black' soils of the Southern Alps, which contain high contents of iron and aluminum oxides and large amounts of fire-derived 'stable' organic matter (Eckmeier and others 2010). Moreover, climate had a considerable effect on SOC storage both in the organic layer and the mineral soil with a negative relation of SOC stocks to MAT in the organic layer, and a positive with MAP in the mineral soil. The strong effects of MAT and MAP on SOC storage are in agreement with numerous other studies (Vesterdal and others 2011; Doblas-Miranda and others 2013; Gabarrón-Galeote and others 2015). These relationships suggest that the expected climate changes with increasing temperatures and higher frequencies of drought (Akademien der Wissenschafften Schweiz 2016) will lead to smaller SOC stock in mountainous regions as it has been observed in warming experiment and repeated soil surveys (Schindlbacher and others 2009; Streit and others 2014; Prietzel and others 2016).

Historical, present, and future land-use change is considered as a main driver of terrestrial C storage (Ciais and others 2013). It is expected that terrestrial ecosystems in the Northern hemisphere currently act as a net C sink (Gutman and others 2012; Janssens and others 2003) due to high afforestation rates, agricultural land abandonment and reduced wood harvest. Soil C modelling suggests that after a change in land management SOC storage follows a sigmoidal increase with the strongest increase after several decades (Jandl and others 2007). Furthermore, a modelling study forest C dynamics for the Swiss Plateau and the Alps by Thürig and Kaufmann (2010) expects that an increasing C input by a reduced forest management will increase SOC stocks for several decades. In recent estimates of the climate balance through forest expansion in mountainous regions, Schwaab and others (2015) showed that C sequestration in biomass and soils is, however, largely outbalanced by an increased radiative forcing through albedo changes under the assumption that forests would accumulate soil C during stand development. Our study strongly suggests—in conjunction with other case studies—that ongoing forest expansion and development in Switzerland and probably also in other mountainous temperate regions in Europe is not associated with an increased C sequestration in soils, deteriorating the climate balance of terrestrial ecosystems. Therefore, we conclude that Switzerland and mountainous countries with similar forest covers and grassland as previous land use influence the European carbon balance to a lesser extent than previously projected and depend on regional variations in the climate, the vegetation, and the soil properties.

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5.1. Compliance with Ethical Standards

Conflict of interest. The authors declare no conflict of interest.

6. REFERENCES

Achat DL, Fortin M, Landmann G, Ringeval B, Augusto L. 2015. Forest soil carbon is threatened by intensive biomass harvesting. Nat Sci Rep 5:15991. doi:10.1038/srep15991.
Akademie der Wissenschaften Schweiz. 2016. Brennpunkt Klima Schweiz. Grundlagen, Folgen und Perspektiven. Swiss Acad Rep 11(5):34–45.

Angst M. 2012. Integration of Nature Protection in Swiss Forest Policy. INTEGRATE Country Report for Switzerland. Country report within the framework of the research project INTEGRATE (Integration of nature protection in forest management and its relation to other functions/services) of the Central European Office of the European Forest Institute (EFICENT), Freiburg I.B. [published online July 2012] Available from World Wide Web http://www.wsl.ch/ publikationen/pdf/11873.pdf. Birmensdorf, Swiss Federal Research Institute for Forest, Snow and Landscape, WSL. 76 S.

Bárcena TG, Kiær LP, Vesterdal L, Stefánsdóttir HM, Gundersen P, Sigurdsson BD. 2014. Soil carbon stock change following afforestation in Northern Europe: a meta-analysis. Glob Change Biol 20:2393–405.

Bolliger J, Hagedorn F, Leifeld J, Bo¨ hl J, Zimmermann S, Soliva R, Kienast F. 2008. Effects of land-use change on carbon stocks in Switzerland. Ecosystems 11:895–907.

Böttcher J, Springob G. 2001. A carbon balance model for organic layers of acid forest soils. J Plant Nutr Soil Sci 164:399–405.

Braun-Blanquet J. 1964. Pflanzensoziologie Grundzüge der Vegetationskunde. 3rd edn. Berlin: Springer.

Brändli U-B (Red.). 2010. Schweizerisches Landesforstinventar. Ergebnisse der dritten Erhebung 2004–2006. Birmensdorf, Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft WSL. Bern, Bundesamt für Umwelt, BAFU. 312 S.

Brändli U-B, Cioldi F, Fischer C, Huber M. 2015. Swiss National Forest Inventory—Special assessments for the Forest Report 2015 in the internet. WSL, Birmensdorf. Online: www.lfi.ch/ publ/waldbericht/2015-en.php [17.8.15].

Ciais P, Sabine C, Bala G et al. 2013. Carbon and other biogeochemical cycles. Climate Change 2013 Physical Science Basis Contribution to Working Group I to Fifth Assessment Report of the Intergovernmental Panel on Climate Change, pp. 465–570. doi:10.1017/CBO9781107415324.014

Crawley MJ. 2007. Regression. The R book. Hoboken: Wiley.

Doblas-Miranda E, Rovira P, Brotons L,Martı´nez-Vilalta J, Retana J, PlaM, Vayreda J. 2013. Soil carbon stocks and their variability across the forests, shrublands and grasslands of peninsular Spain. Biogeosciences 10:8353–61. doi:10.5194/bg-10-8353-2013.

Dupouey JL, Dambrine E, Laffite JD, Moares C. 2002. Irreversible impact of past land use on forest soils and biodiversity. Ecology 83(11):2978–84. doi:10.2307/3071833.

Eckmeier E, Egli M, Schmidt MWI, Schlumpf N, Nötzli M, Minikus-Stary N, Hagedorn F. 2010. Preservation of fire-derived carbon compounds and sorptive stabilisation promote the accumulation of organic matter in black soils of the Southern Alps. Geoderma 159:147–55.

FOEN. 2012. Switzerland's Greenhouse Gas Inventory 1990- 2010. National Inventory Report 2012 including reporting elements under the Kyoto Protocol; Federal Office for the Environment Bern.

Fuchs R, Schulp CJE, Hengeveld GM, Verburg PH, Clevers JGPW, Schelhaas M-J, Herold M. 2016. Assessing the influence of historic net and gross land changes on the carbon fluxes of Europe. Glob Change Biol 22:2526–39. doi:10.1111/gcb.13191.

Gabarrón-Galeote MA, Trigalet S, van Wesemael B. 2015. Effect of land abandonment on soil organic carbon fractions along a Mediterranean precipitation gradient. Geoderma 249–250:69–78. doi:10.1016/j.geoderma.2015.03.007.

Gee GW, Bauder JW. 1986. Particle-size analysis. In: Klute A, Ed. Methods of soil analysis. Part 1. 2nd ed. Agronomy monograph 9. Madison, WI: ASA and SSSA. pp. 383–411.

Gellrich M, Baur P, Zimmermann NE. 2007. Natural forest regrowth as a proxy variable for agricultural land abandonment in the Swiss mountains: a spatial statistical model based on geophysical and socio-economic variables. Environ Model Assess J 12:269–78. doi:10.1007/s10666-006-9062-6.

Gimmi U, Poulter B, Wolf A, Portner H, Weber P, Bürgi M. 2013. Soil carbon pools in Swiss forests show legacy effects from historic forest litter raking. Landsc Ecol 28:835–46.

Ginzler C, Brändli UB, Ha¨ geli M. 2011. Waldflächenentwicklung der letzten 120 Jahre in der Schweiz. Schweiz Z Forstwes162:337–43.

Gnägi C, Labhart T. (2015) Geologie der Schweiz, 9, vollständig überarbeitete Auflage, ott verlag, 208 Seiten. ISBN 978-3-7225-0142-0.

Gonseth Y, Wohlgemuth T, Sansonnens B, Buttler A. 2001. Die biogeographischen Regionen der Schweiz. Erläuterungen und Einteilungsstandard. Bern: Bundesamt fu¨ r Umwelt Wald und Landschaft.

Guidi C, Vesterdal L, Gianelle D, Rodeghiero M. 2014. Changes in soil organic carbon and nitrogen following forest expansion on grassland in the Southern Alps. For Ecol Manag 328:103–16.

Guillaume T, Damris M, Kuzyakov Y. 2015. Losses of soil carbon by converting tropical forest to plantations: erosion and decomposition estimated by a13C. Glob Change Biol 21:3548–60. doi:10.1111/gcb.12907.

Guo LB, Gifford RM. 2002. Soil carbon stocks and land use change: a meta-analysis. Glob Change Biol 8:345–60.

Gutman G et al., Eds. 2012. Land change science. Remote sensing and digital image processing, vol 6. doi:10.1007/978-1-4020-2562-4_14.

Hagedorn F, Moeri A, Walthert L, Zimmermann S. 2010. Kohlenstoff in Schweizer Waldböden—bei Klimaerwärmung eine potenzielle CO2—Quelle. Schweizerisch Zeitschrift für Forstwesen 161(12):530–5.

Harrell FE Jr, et al., with contributions from C. D. and many. 2015. Hmisc: Harrell Miscellaneous. R package version 3.16-0. http://cran.r-project.org/package=Hmisc.

Heiberger RM. 2015. HH: Statistical analysis and data display: Heiberger and Holland. R package version 3.1-21. at http://cran.r-project.org/package=HH.

Hiltbrunner D, Zimmermann S, Hagedorn F. 2013. Afforestation with Norway spruce on a subalpine pasture alters carbon dynamics but only moderately affects soil carbon storage. Biogeochemistry 115:251–66.

IUSS Working Group WRB. 2007. World Reference Base for Soil Resources 2006, first update 2007, World Soil Resources Reports No. 103, FAO, Rome.

Jandl R, Lindner M, Vesterdal L et al. 2007. How strongly can forest management influence soil carbon sequestration? Geoderma 137:253–68.

Janssens IA, Freibauer A, Ciais P et al. 2003. Europe's terrestrial biosphere absorbs 7 to 12% of European anthropogenic CO2 emissions. Science 300(5625):1538–42. doi:10.1126/science. 1083592.

Kümmerle T, Kaplan JO, Prishchepov AV, Rylsky I, Chaskovskyy O, Tikunov VS, Mu¨ ller D. 2015. Forest transitions in Eastern Europe and their effects on carbon budgets. Glob Change Biol 21:3049–61. doi:10.1111/gcb.12897.

Lal R. 2005. Forest soils and carbon sequestration. For Ecol Manag 220:242–58.

Lemon J. 2006. Plotrix: a package in the red light district of R. RNews 6:8–12.

Lettens S, Van Orshoven J, van Wesemael B, Perrin D, Roelandt C. 2004. The inventory-based approach for prediction of SOC change following land use change. Biotechnol, Agron, Soc Environ (BASE) 8(2):141–6.

Liski J, Perruchoud D, Karjalainen T. 2002. Increasing carbon stocks in the forest soils of western Europe. For Ecol Manag 169(1–2):159–75.

Lorenz K, Lal R. 2010. Carbon sequestration in forest ecosystems. Berlin: Springer. doi:10.1007/978-90-481-3266-9_1

Mobley ML, Lajtha K, Kramer MG, Bacon AR. 2015. Surficial gains and subsoil losses of soil carbon and nitrogen during secondary forest development. Glob Change Biol 21:986–96. doi:10.1111/gcb.12715.

Motzkin J, Bellemare G, Foster DR. 2002. Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. J Biogeogr 29:1401–20.

Neuwirth E. (2014) RColorBrewer: ColorBrewer Palettes. R package version 1.1-2. http://cran.r-project.org/package=RColorBrewer.

Nussbaum M, Papritz A, Zimmermann S, Wathert S. 2016. Pedotransfer function to predict denisty of forest soils in Switzerland. J Plant Nutr Soil Sci 179:321–6. doi:10.1002/jpln. 201500546.

Paul KI, Polglase PJ, Nyakuengama JG, Khanna PK. 2002. Change in soil carbon following afforestation or reforestation. For Ecol Manag 168:241–57.

Peltoniemi M, Mäkipää R, Liski J, Tamminen P. 2004. Changes in soil carbon with stand age—an evaluation of a modelling method with empirical data. Glob Change Biol 10:2078–91. doi:10.1111/j.1365-2486.2004.00881.x.

Poeplau C, Don A, Vesterdal L, Leifeld J, van Wesemaels B, Schumacher J, Gensior A. 2011. Temporal dynamics of soil organic carbon after land-use change in the temperate zone—carbon response functions as a model approach. Glob Change Biol 17:2415–27.

Poeplau C, Don A. 2013. Sensitivity of soil organic carbon stocks and fractions to different land-use changes across Europe. Geoderma 192:189–201. doi:10.1016/j.geoderma.2012.08.003.

Prietzel J, Zimmermann L, Schubert A, Christophel D. 2016. Organic matter losses in German Alps forest soils since the 1970s most likely caused by warming. Nat Geosci 9:543–8. doi:10.1038/NGEO2732.

Remund J, Rihm B, Huguenin-Landl B. 2014. Klimadaten für die Waldmodellierung für das 20. und 21. Jahrhundert Schlussbericht. Forschungsprogramm ,,Wald und Klimawandel“ des Bundesamtes für Umwelt BAFU, Bern und der Eidg. Forschungsanstalt WSL, Birmensdorf. Meteotest, Bern.

R Core Team. 2015. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. https://www.r-project.org/.

Ripley B. 2015. Tree: classification and regression trees. R package version 1.0-36. http://cran.r-project.org/package=tree.

Rounsevell MD, Annetts J, Audsley E, Mayr T, Reginster I. 2003. Modelling the spatial distribution of agricultural land use at the regional scale. Agr Ecosyst Environ 95:465–79.

Rounsevell MD, Reginster I, Arau´ jo MB et al. 2006. A coherent set of future land use change scenarios for Europe. Agr Ecosyst Environ 114:57–68.

Scharlemann JPW, Tanner EVJ, Hiederer R, Kapos V. 2014. Global soil carbon: understanding and managing the largest terrestrial carbon pool. Carbon Manag 5(1):81–91. doi:10. 4155/cmt.13.77.

Schindlbacher A, Zechmeister-Boltenstern S, Jandl R. 2009. Carbon losses due to soil warming: do autotrophic and heterotrophic soil respiration respond equally? Glob Change Biol 15(4):901–13. doi:10.1111/j.1365-2486.2008.01757.x.

Schmidt MWI, Torn MS, Abiven S et al. 2011. Persistence of soil organic matter as an ecosystem property. Nature 478:49–56.

Schulp CJE, Verburg PH. 2009. Effect of land use history and site factors on spatial variation of soil organic carbon across a physiographic region. Agr Ecosyst Environ 133:86–97.

Schwaab J, Bavay M, Davin E et al. 2015. Carbon storage versus albedo change: radiative forcing of forest expansion in temperate mountainous regions of Switzerland. Biogeosci Discuss 11:10123–65.

Sjögersten S, Alewell C, Cécillon L et al. 2011. Mountain soils in a changing climate—vulnerability of carbon stocks and ecosystem feedbacks. Soil Carbon Sensit Eur Ecosyst From Sci Land Manag. doi:10.1002/9781119970255.ch6.

Spielvogel S, Prietzel J, Kögel-Knabner I. 2006. Soil organic matter changes in a spruce ecosystem 25 years after disturbance. Soil Sci Soc Am J 70:2130–45. doi:10.2136/sssaj2005.0027.

Streit K, Hagedorn F, Hiltbrunner D, Portmann M, Saurer M, Buchmann N, Wild B, Richter A, Wipf S, Siegwolf RTW. 2014. Soil warming alters microbial substrate use in alpine soils. Glob Change Biol 20(4):1327–38. doi:10.1111/gcb.12396.

Swisstopo. 2011. DEM, Swisstopo.

Thuille A, Schulze E-D. 2006. Carbon dynamics in successional and afforested spruce stands in Thuringia and the Alps. Glob Change Biol 12:325–42. doi:10.1111/j.1365-2486.2005.01078.x.

Thürig E, Kaufmann E. 2010. Increasing carbon sinks through forest management: a model-based comparison for Switzerland with its Eastern Plateau and Eastern Alps. Eur J For Res 129:563–72. doi:10.1007/s10342-010-0354-7.

Venables WN, Ripley BD. 2002. Modern applied statistics with S. 4th edn. New York: Springer.

Vesterdal L, Ritter E, Gundersen P. 2002. Change in soil organic carbon following afforestation of former arable land. For Ecol Manag 169(1–2):137–47.

Vesterdal L, Leifeld J, Poeplau C, Don A, van Wesemael B. 2011. Land-use change effects on soil carbon stocks in temperate regions—development of carbon response functions. In: Jandl R, Rodeghiero M, Olsson M, Eds. Soil carbon in sensitive european ecosystems: from science to land management. Chichester: Wiley. doi:10.1002/9781119970255.ch3

Vesterdal L, Clarke N, Sigurdsson BD, Gundersen P. 2013. Do tree species influence soil carbon stocks in temperate and boreal forests? For Ecol Manag 309:4–18. doi:10.1016/j.foreco.2013.01.017.

Walthert L, Graf U, Kammer A, Luster J, Pezzotta D, Zimmermann S, Hagedorn F. 2010. Determination of organic and inorganic carbon, d13C, and nitrogen in soils containing carbonates after acid fumigation with HCl. J Plant Nutr Soil Sci 173:207–16.

Walthert L, Graf Pannatier E, Meier ES. 2013. Shortage of nutrients and excess of toxic elements in soils limit the distribution of soil-sensitive tree species in temperate forests. For Ecol Manag 297:94–107.

Wickham H. 2007. Reshaping data with the reshape package. J Stat Softw 21:1–20.

Wickham H. 2009. ggplot2: elegant graphics for data analysis. New York: Springer.

Wickham H. 2011. The Split-Apply-Combine Strategy for Data Analysis. J Stat Softw 40:1–29.

Wickham H. 2015. tidyr: Easily Tidy Data with ‘spread()‘ and ‘gather()‘ Functions. R package version 0.3.1. http://cran.rproject.org/package=tidyr.

Wickham H. and Francois R. 2015. dplyr: a grammar of data manipulation. R package version 0.4.3. http://cran.r-project. org/package=dplyr.

Wiesmeier M, Spörlein P, Geuß U et al. 2012. Soil organic carbon stocks in southeast Germany (Bavaria) as affected by land use, soil type and sampling depth. Glob Change Biol 18(7):1365–2486. doi:10.1111/j.1365-2486.2012.02699.x.

Wiesmeier M, Prietzel J, Barthold F et al. 2013. Storage and drivers of organic carbon in forest soils of southeast Germany (Bavaria)—implications for carbon sequestration. For Ecol Manag 295:162–72.

Wiesmeier M, Barthold F, Spörlein P et al. 2014. Estimation of total organic carbon storage and its driving factors in soils of Bavaria (southeast Germany). Geoderma Reg 1:67–78. doi:10. 1016/j.geodrs.2014.09.001.

Wäldchen J, Schulze E-D, Schöning I, Schrumpf M, Sierra C. 2013. The influence of changes in forest management over the past 200 years on present soil organic carbon stocks. For Ecol Manag 289:243–54.

7. APPENDIX

Supplementary Table 1: SOC stocks according to forest age and forest type for organic layer, mineral soil, and total SOC stocks.

SOC stocks (in kg C m^{-2}) according to forest age categories and forest type (means ± standard errors)				
SOC stocks	**< 60**	**60-120**	**> 120**	**Forest type**
Organic Layer	1.1±0.2 (n=32)	1.4±0.2 (n=87)	0.9±0.06 (n=296)	Broadleaf
	3.6±0.7 (n=35)	4.3±0.6 (n=107)	3.6±0.3 (n=278)	Conifer
Mineral Soil (0-120 cm)	13.4±1.7 (n=32)	12.2±0.7 (n=87)	10.2±0.3 (n=296)	Broadleaf
	11.8±1.1 (n=35)	10.6±0.6 (n=107)	10.9±0.4 (n=278)	Conifer
Total C stocks	14.5±1.7 (n=32)	13.6±0.8 (n=87)	11.1±0.3 (n=296)	Broadleaf
	15.3±1.1 (n=35)	14.9±0.7 (n=107)	14.5±0.5 (n=278)	Conifer

Supplementary Table 2: ANOVA models indicating order of variables used for the analysis.

Table 2	**ANOVA (with function aov.ko)**
Organic layer	summary(model <- aov.ko(log-transformed(organic layer) ~ Region*Soil group + BC*Soil group + Forest age*Soil group + MAT + pH*Forest type, data=Forest age)
Mineral soil	summary(model <- aov.ko(log-transformed(mineral soil) ~ Region*Soil group + Forest age*Soil group + MAP + Slope + Altitude + Sand content + BC*Soil group + Soil type*BC + Forest type, data=Forest age)
Total C stocks	summary(model <- aov.ko(log-transformed(total C stocks) ~ Region*Soil group + Forest age*Soil group + BC + BC*Soil group + Relief + Forest type + Slope + MAP + MAT, data= Forest age)
The sign "*" denotes an interaction between two covariates. Fitted models are not shown.	

Supplementary Table 3: Results from post-hoc TukeyHSD tests comparing the means of the three forest age categories.

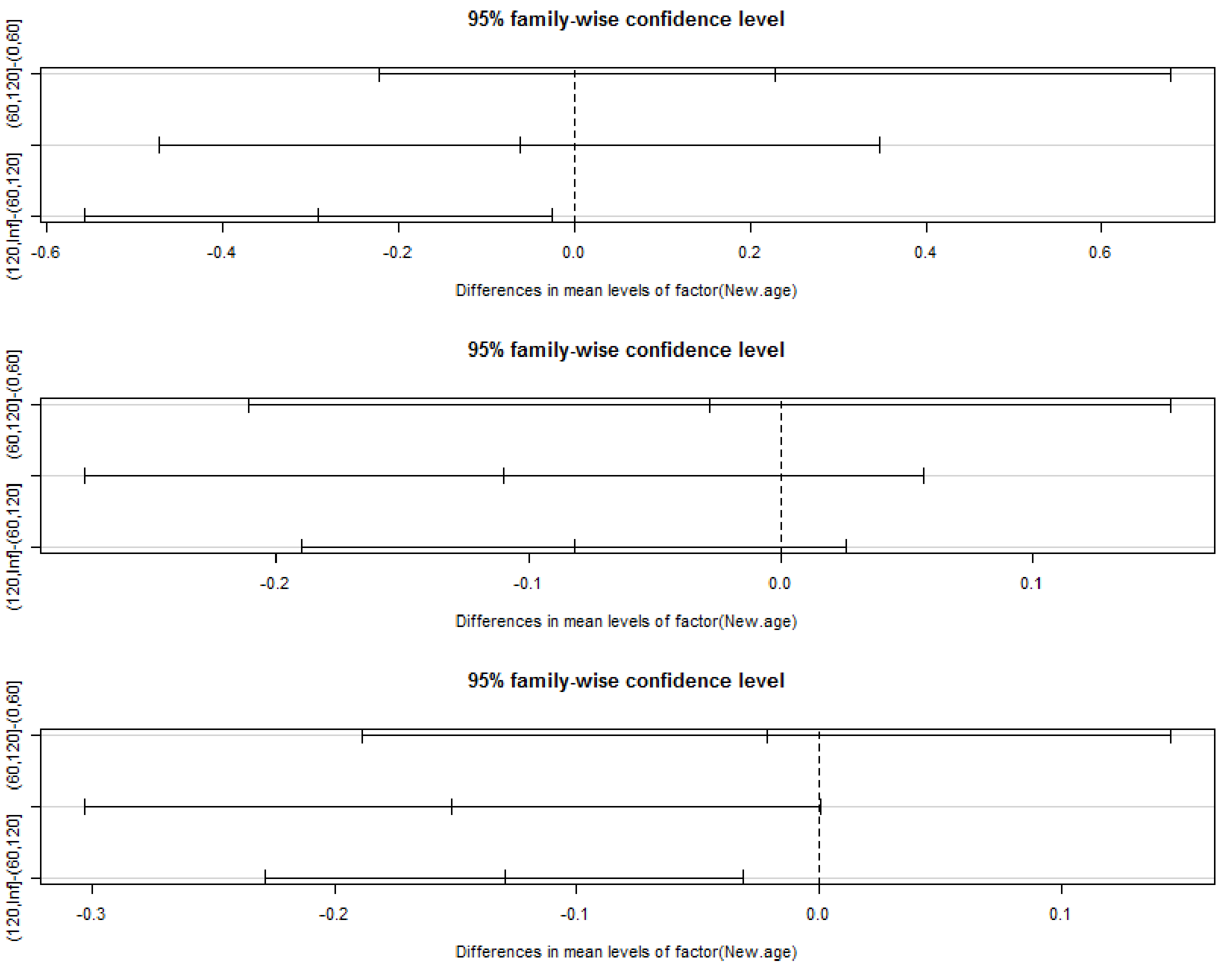
Table 3	**TukeyHSD post-hoc tests** Tukey multiple comparisons of means 95% family-wise confidence interval				
	Forest age comparison	**Diff**	**Lwr**	**Upr**	**P adj**
Organic layer	Medium - Young	0.23	-0.22	0.68	0.5
	Old - Young	-0.06	-0.47	0.35	0.9
	Old - Medium	-0.29	-0.56	-0.03	**0.03**
Mineral soil	Medium - Young	-0.03	-0.21	0.16	0.9
	Old - Young	-0.11	-0.27	0.06	0.26
	Old - Medium	-0.08	-0.18	0.03	0.17
Total C stocks	Medium - Young	-0.02	-0.19	0.15	0.9
	Old - Young	-0.15	-0.30	0.00	**0.05**
	Old - Medium	-0.13	-0.23	-0.03	**0.006**
Confidence level is 0.95, data presents lower and upper limits, their average and the adjusted p-values.					

Supplementary Table 4: ANOVA results on the effect of forest age and other variables on SOC stocks for the five biogeographic regions of Switzerland.

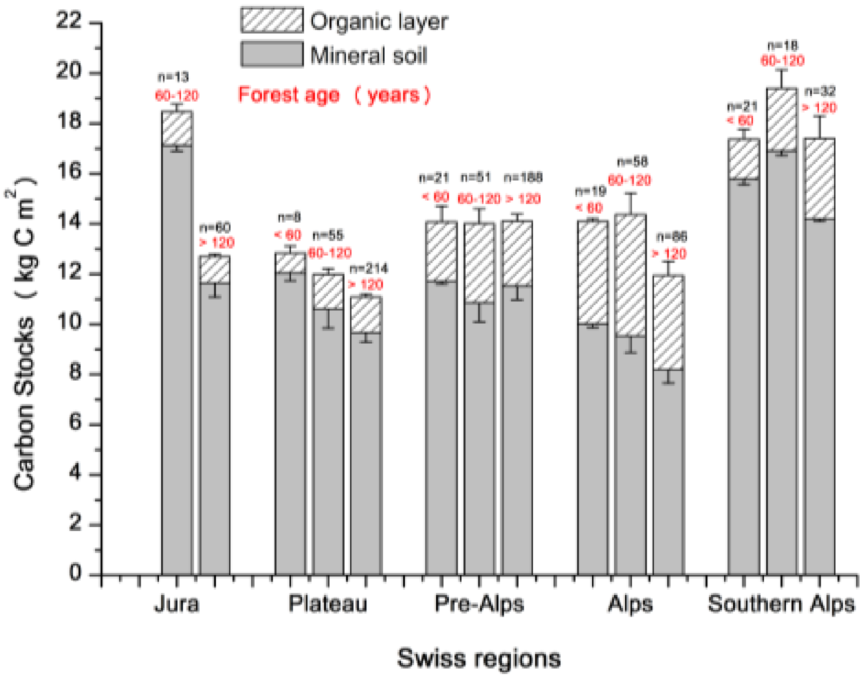
Region	Organic Layer				Mineral Soil			
	Covariate	**Df**	**SS (%)**	**F**	**Covariate**	**Df**	**SS (%)**	**F**
Jura	Soil group	2	19.2	$F_{(2,65)}$ = 9.952 ***	Soil group	2	14.6	$F_{(2,66)}$ = 7.847 ***
	pH	1	3.1	$F_{(1,65)}$ = 3.191 .	BC	1	12.3	$F_{(1,66)}$ = 13.218 ***
	Soil group x BC	3	14.9	$F_{(3,65)}$ = 5.164 **	Forest type	1	5.1	$F_{(1,66)}$ = 5.493 *
	-	-	-	-	Slope	1	6.3	$F_{(1,66)}$ = 6.775 *
	Residuals	65	62.8	-	Residuals	66	61.7	-
Swiss Plateau	Soil group	2	14.4	$F_{(2,264)}$ = 33.476 ***	Soil group	2	8.2	$F_{(2,263)}$ = 16.311 ***
	BC	1	9.5	$F_{(1,264)}$ = 44.422 ***	BC	1	5.5	$F_{(1,263)}$ = 21.924 ***
	MAT	1	1.0	$F_{(1,264)}$ = 4.536 *	Slope	1	8.8	$F_{(1,263)}$ = 35.189 ***
	pH	1	7.3	$F_{(1,264)}$ = 33.867 ***	MAP	1	5.6	$F_{(1,263)}$ = 22.325 ***
	Forest type	1	3.5	$F_{(1,264)}$ = 16.415 ***	Soil group x BC	2	2.7	$F_{(2,263)}$ = 5.412 **
	Soil group x BC	2	5.9	$F_{(2,264)}$ = 13.784 ***	Soil group x Forest age	6	3.3	$F_{(6,263)}$ = 2.171 *
	pH x Forest type	1	1.7	$F_{(1,264)}$ = 7.842 **	-	-	-	-
	Residuals	264	56.7	-	Residuals	263	65.9	-
Pre-Alps	Soil group	2	13.3	$F_{(2, 248)}$ = 38.980 ***	Soil group	2	5.0	$F_{(2,251)}$ = 8.551 ***
	BC	1	18.3	$F_{(1,248)}$ = 106.945 ***	BC	1	4.7	$F_{(1,251)}$ = 16.126 ***
	MAT	1	4.2	$F_{(1, 248)}$ = 24.537 ***	Forest type	1	6.9	$F_{(1,251)}$ = 23.534 ***
	pH	1	9.0	$F_{(1, 248)}$ = 52.696 ***	Slope	1	3.0	$F_{(1,251)}$ = 9.904 **
	Forest type	1	1.7	$F_{(1, 248)}$ = 9.826 **	MAP	1	6.8	$F_{(1,251)}$ = 23.293 ***
	Soil group x BC	2	7.7	$F_{(2, 248)}$ = 22.472 ***	-	-	-	-
	pH x Forest type	1	3.3	$F_{(1, 248)}$ = 19.088 ***	-	-	-	-
	Residuals	248	42.5	-	Residuals	251	73.6	-
Alps	Soil group	2	8.4	$F_{(2, 156)}$ = 9.176 ***	Soil group	2	5.9	$F_{(2,155)}$ = 7.190 **
	BC	1	10.9	$F_{(1, 156)}$ = 23.876 ***	BC	1	13.7	$F_{(1,155)}$ = 32.795 ***
	MAT	1	2.3	$F_{(1, 156)}$ = 4.902 *	Forest age	2	2.5	$F_{(1,155)}$ = 3.032 .
	pH	1	3.4	$F_{(1, 156)}$ = 7.431 **	Slope	1	2.7	$F_{(1,155)}$ = 6.397 **
	Forest type	1	3.7	$F_{(1, 156)}$ = 8.190 **	MAP	1	10.6	$F_{(1,155)}$ = 25.347 ***
	Residuals	156	71.3	-	Residuals	155	64.6	-
Southern Alps	MAT	1	23.0	$F_{(1,65)}$ = 26.568 ***	Soil group	2	6.4	$F_{(2,65)}$ = 2.756 .
	pH	1	8.0	$F_{(1,65)}$ = 9.227 **	MAP	1	3.4	$F_{(1,65)}$ = 2.935 .
	Soil group x BC	3	12.7	$F_{(3,65)}$ = 4.880 **	Soil group x BC	2	14.7	$F_{(1,65)}$ = 6.330 **
	Residuals	65	56.3	-	Residuals	65	75.5	-

The abbreviation df stands for degrees of freedom, SS represents the sum of squares in %, F represents the F-value. The annotation (“-”) means that the variable was not present in the final model fit.

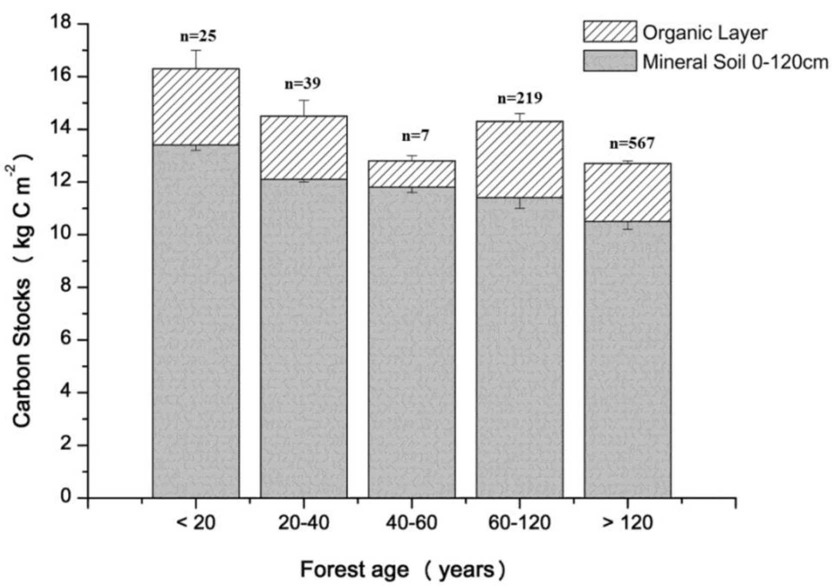
Supplementary Figure 1: TukeyHSD plots comparing the means of the three different forest categories for C stocks in organic layer, mineral soil (0-120 cm soil depth), and total C stocks (top to bottom). Lines represent the differences in means between forest age groups (from top to bottom: medium vs. young, old vs. young, and old vs. medium, respectively). If a line crosses the 0.0 dashed mark, there is no significant difference between the means of the examined groups, if it does not – there is a significant difference.



Supplementary Figure 2: Distribution of SOC stocks (kg C m^2) according to the five bio-geographic regions of Switzerland (top dashed: organic layer, bottom grey: mineral soil at 0-120 cm soil depth), sub-divided by forest age categories (in red). Whiskers indicate standard errors, numbers above forest age categories – number of sites per forest age category. The category 'young forests' was not present in the region of Jura.



Supplementary Figure 3: Distribution of SOC stocks (kg C m2) according to a more detailed separation of forest age (top dashed: organic layer, bottom grey: mineral soil at 0-120 cm soil depth). Whiskers indicate standard errors, numbers above forest age categories – number of sites per forest age category.



Paper II

SOM storage and pool distribution in forest soils along climatic gradients across Switzerland

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ABSTRACT

Soil organic matter (SOM) consists of a continuum of compounds ranging from slightly altered plant residues, known as particulate OM (POM) to the relatively more stable mineral-associated OM (MOM). POM is the most rapidly cycling and hence responsive fraction of SOM. In this study, we investigate the effect of different climatic conditions and soil chemistry along a natural elevational gradient in Swiss mountains on SOC storage and SOM quality of different SOM fractions in forest soils. Using density fractionation, 54 mineral soils (soil depth 0-20 cm) were separated into their organic horizons, free and occluded light, and coarse and fine heavy fractions. SOC stocks, C/N ratio, and the $\delta^{13}C$ and $\delta^{15}N$ values were measured.

There was an increase in ^{13}C and ^{15}N from plant residues in the organic layer and from roots to the light and heavy fractions in the mineral soil, reflecting SOM decomposition. However, while the C/N ratio significantly decreased from roots to the light and heavy fraction of the mineral soil, it remained similar from the organic layer towards these fractions. As C/N ratios narrows with decomposition, this pattern strongly suggest that the organic layer does hardly contribute to the mineral associated SOM. In turn, our findings imply that above-ground litter inputs make only a small contribution to long-term C sequestration in mineral-associated SOM. There was only an insignificant and inconsistent effect of climatic conditions on SOM pools. The contribution of total POM (organic layer + light fraction) to SOM was greatest in warm-moist climatic conditions (72.3%) and smallest in cold-moist ones (62.8%). In comparison, soil chemical properties were significantly related to SOC stocks, the pool distribution and the C/N ratio as well as $\delta^{15}N$ values. Consequently, the direct effect of climate was only minor, whereas soil chemistry had a more dominant effect on both SOC stocks and SOM quality.

Keywords: Particulate Organic Matter, Fractionation, Climatic gradients, Forest soils, $\alpha^{13}C$ and $\alpha^{15}N$ isotopic ratios, SOC storage

1. INTRODUCTION

Soil organic matter (SOM) is responsible for numerous soil ecosystem functions – it stores carbon (C), influences soil biodiversity and is a source of key soil nutrients. Forest soils contain particularly high soil organic carbon (SOC) stocks (Lal, 2005; Smith, 2008; Lorenz and Lal, 2010; Blume et al., 2016). Especially temperate forest soils in central Europe, such as the ones in Switzerland, are believed to have a high potential to sequester C (Wiesmeier et al., 2013). SOC stocks result from in- and outputs of C in soils (Bellamy et al., 2005; Davidson and Janssens, 2006; Smith, 2008), which can be influenced by several processes such as net primary production (for C inputs) or soil respiration (for C outputs). Furthermore, any changes in climate could affect the C balance in soils, e.g., climate warming could lead to an enhanced mineralization of SOM, a temperature-dependent process, which may turn soils into a source of CO_2 (Hagedorn et al., 2010; Bradford et al., 2016). Many different physical, chemical, and biochemical processes support the stabilization of SOM (Six et al., 2002; Kayler et al., 2011; Schmidt et al., 2011), leading to C accumulation in soils. Presently, however, there are still many uncertainties regarding the driving processes behind stabilization and destabilization mechanisms of SOM (Schmidt et al., 2011), especially if we consider individual SOM functional pools (Hoyle et al., 2016).

SOM consists of a complex continuum of compounds at different stages of decomposition and with a different mean residence time and stability. Slightly altered plant residues, known as particulate OM (POM) are considered to be more labile, whereas mineral-associated OM (MOM) contains more stable C (Schrumpf et al., 2013). Therefore, climate or land-use disturbances are more likely to have a stronger impact on SOM in the organic layer and the POM, as compared to the more stable MOM. However, a detailed understanding on changes of SOM in the labile vs. the stable fractions remains unclear. This might be due to the fact that SOM is stabilized by different stabilization mechanisms (von Lützow et al., 2007). Such mechanisms, however, can be further affected by climatic changes, hindering therefore a precise prediction of how SOM would respond to changes. However, SOM quality can be investigated through the C/N ratio, in terms of decomposability of OM. Furthermore, since isotopic ratios of ^{13}C to ^{12}C ($\delta^{13}C$) and ^{15}N to ^{14}N ($\delta^{15}N$) differ between SOM fractions (lower $\delta^{13}C$ in the organic layer and POM as compared to MOM (Torn et al., 2009)), examining these will allow an estimation of the stability of SOC (Gunina and Kuzyakov, 2014).

Despite the importance of SOC dynamics in forest ecosystems, our understanding regarding the individual SOM fractions is still incomplete, as compared to other ecosystems. In grassland soils, for example, SOM content, as well as the contribution of POM, were found to increase with increasing elevation (Leifeld et al., 2009), suggesting that climate exerts a major control on

SOM stability. Climate, in particular increasing precipitation, was furthermore found to exert a positive effect on POM in a temperate steppe region (Song et al., 2012). For dryland agricultural systems in Australia, (Hoyle et al., 2016) demonstrated climate to be among the strongest explanatory factors of SOC. Although there are some studies of SOM stability in temperate forest soils (Schrumpf et al., 2013) where a substantial fraction of POM is stored in the organic layer, less has been researched at locations with an existing natural elevational gradient. SOC storage is associated with altitudinal changes; specifically, SOC stocks increase with elevations due to lower microbial activity and thus smaller C outputs (Garten Jr, 2004; Sjögersten et al., 2011). Furthermore, the existing elevational gradient in Switzerland is associated with diversity in climatic conditions, vegetation cover, and topography.

In our study, we investigate the effect of climate, tree species composition, and soil physical and chemical properties on SOC storage and SOM distribution in the organic layer and within the top 20 cm of mineral soils of 54 Swiss forest soil profiles distributed along a natural elevational gradient. We postulate that changes in climatic conditions, corresponding to an elevational increase, will have a minor effect on total SOC storage; however, we expect to find a pronounced effect of climate on SOM quality (contribution of POM to SOM stocks and C/N ratio, see *Fig. 1*). We addressed the following objectives: 1.) to examine trends of SOC stocks, C/N and isotopic ratios in different fractions; 2.) to examine the effect of different climatic conditions along a natural elevational gradient on total SOC storage; and 3.) to assess the effect of climate and soil properties on SOM quality of different SOM fractions.

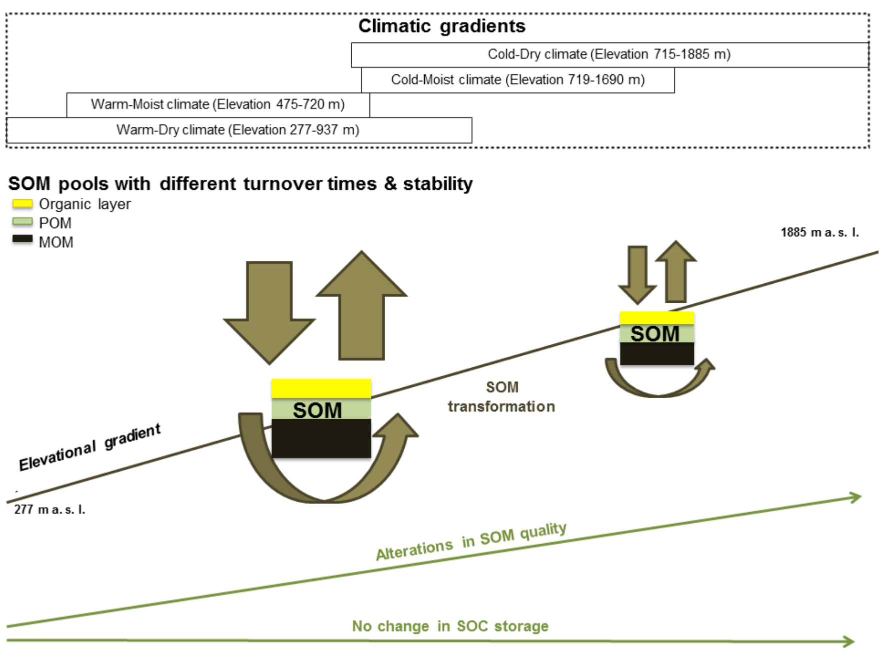

Fig. 1: Graphical representation of the hypothesis of the study.

2. MATERIAL AND METHODS

2.1. Study area, site selection and sampling

Switzerland is divided into five biogeographic regions (*Fig. 2*): Jura (n=11), Plateau (n=15), Pre-Alps (n=9), Alps (n=13), and the Southern Alps (n=6). Each of the regions exhibits different bedrock and climatic conditions. The Jura, the Plateau, and the Pre-Alps are characterized by a temperate humid climate, whereas the Alps have a wet continental climate and the Southern Alps exhibit warm climatic conditions (Gonseth et al., 2001). Calcareous bedrock is found mainly in the Jura, whereas the Southern Alps are characterized by acidic bedrock. The other three regions have very heterogeneous bedrocks, as e.g. calcareous moraines found in the Plateau or calcareous sediments found in the Pre-Alps (Gnägi and Labhart, 2015).

Fig. 2. Distribution of forest sites according to biogeographic regions in Switzerland (n=54).

Altogether, 54 sites were selected based on an ecosystem variability procedure, divided into four climatic ecosystems: warm-moist, warm-dry, cold-moist, and cold-dry. The selection was defined according to mean monthly temperatures (below and above 8.51°C) and a soil moisture index (less than and more than 47 dry months). The organic layer and the top mineral soil (at a soil depth 0-20 cm) were sampled in the summer of 2014. Per site, three composites were selected (40 x 40 m^2) and for each composite, eight soil cores were sampled and afterwards mixed together to dampen spatial variability (for further details on soil sampling and ecosystem variability procedure, please see González Domínguez et al., (*in prep.*).

In addition, information on the corresponding mineral soil (at soil depth 0-120 cm) forest sites was available from the soil database of the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL) and was included in the analysis.

2.2. Environmental variables

The selected sites span an elevational gradient from 277 to 1885 m a.s.l. The four climatic conditions were used as a proxy of the natural existing elevational gradient in Switzerland. Clay contents were determined by the sedimentation method according to Gee and Bauder (1986) and classified into five groups: 0-10%, 10-15%, 15-20%, 20-30%, and > 30%. The mean average values of pH were calculated by weighting the averages of the contents with the amount of fine earth. Plant species in herb, shrub and tree layers were determined using the Braun-Blanquet cover abundance scale (Braun-Blanquet, 1964). Based on this scale, broadleaf percentage was calculated as the sum of the cover of all broadleaf species divided by the sum of the cover of all tree species at canopy level. Finally, forest type was divided into conifer (0-50%) and broadleaf (51-100%).

2.3. Density fractionation

The organic layer was separated according to horizons (L-F-H). In addition, roots found in the organic layer were also measured. Mineral soils were separated into light (LF) and heavy (HF) fractions. POM is represented by free and occluded light fractions (total POM represents the organic layer and the two light fractions), whereas fine and coarse heavy fractions characterize MOM. The mineral soils of the samples were fractionated according to the method of Griepentrog et al., (2014). The bulk soil was separated into two light fractions: a free light fraction (fLF) and an occluded light fraction (oLF), whereas heavy fractions were separated into a coarse heavy fraction and a fine heavy fraction (cHF and fHF, respectively). The free LF fraction was extracted using a sodium polytungstate solution with a cut-off density of 1.6 g/cm^3 (indicated as the most suitable density for separating the maximum C content in light fractions by Griepentrog et al., (2014) and Cerli et al., (2012)). After 10 minutes of centrifuging at 4000 rpm (Megafuge 1.0, Heraeus), free LF was collected by pouring the floating material through a vacuum filtration. Ultrasonic dispersion energy (300 J/mL) was used to separate the occluded LF fraction. The remaining soil was refilled in the centrifuge tube with a total of 70 mL sodium polytungstate, where it settled for 15 minutes and after dispersion took place, samples were cooled in an ice bath to prevent thermal interferences. The remaining bulk material was separated by particle size fractionation of 20µm into coarse (> 20µm) and fine (< 20µm) HF via wet sieving applied for a period of five minutes. The remains in the sieve represents the coarse HF fraction, while the fine HF fraction was collected after a week of sedimentation (González Domínguez et al., (*in prep.*)).

2.4. Determination of $\delta^{13}C$ isotopes and $\delta^{15}N$ isotopes

All fractions were filled into silver capsules and were weighed according to their C and N contents. To remove all carbonates from the soil, samples with a pH > 6 were fumigated with HCl according to the method of Walthert et al., (2010). The $\delta^{13}C$ and $\delta^{15}N$ isotopes were measured with the Elemental Analysis - Isotope Ratio Mass Spectrometer (IRMS-EA). The isotope ratios were expressed relatively to Vienna Pee Dee Belemnite (VPDB, for $\delta^{13}C$, *equation [1]*) and to air (for $\delta^{15}N$, *equation [2]*).

$$[1] \qquad \delta^{13}C = \left(\frac{Rcsample}{RcVPDB} - 1\right) \times 1000‰ Rc = \frac{13c}{12c}$$

$$[2] \qquad \delta^{15}N = \left(\frac{R_N sample}{R_N Air} - 1\right) \times 1000‰ R_N = \frac{15_N}{14_N}$$

Whereas isotopic ratios in the mineral soils were measured according to the fractions, these were measured for single layers in the organic layer (L, F, H horizons) and for roots found in the organic layer. Furthermore, enrichment factors between LF and HF were calculated for both $\delta^{13}C$ and $\delta^{15}N$ to examine the fractionation during decomposition. The factors were calculated used the following formula (*equation [3]*):

$$[3] \qquad \varepsilon = \frac{(\delta^{13}C_{HF} - \delta^{13}C_{LF})}{ln\left(\frac{SOC_{HF}}{SOC_{LF}}\right)}$$

where ε is the Ray Raleigh enrichment factor, SOC_{HF} and SOC_{LF} represent C concentrations in the heavy and light fractions, respectively.

2.5. Calculation of SOC stocks

For the organic layer, SOC stocks were calculated multiplying the sample's dry weight (in g), its C concentration, and an area extrapolation factor (EF) to account for the area for the single horizons. The dry weight of the samples was comprised of the sum of the subsamples, totalling from the weighted subsamples and summed up to obtain the final dry weight per sample. Finally, SOC stocks of the single horizons were summed up to obtain total SOC stocks per sample.

During density fractionations, a certain amount of soil weight is lost. Therefore, we first corrected for the fraction weight before calculating SOC stocks in the mineral soil ($SOC\ stocks_{fr}$, *equation [4]*), using the following equation:

$$[4] \qquad SOCstocks_{fr} = \frac{\left\{\frac{W_{fr}}{W_s}\right\}}{\rho} \times TOC\ ,$$

where W_{fr} corresponds to fraction weight, W_s – to sample weight (both in grams), TOC is the concentration of total organic carbon (in g/kg) and ρ is the fine earth amount (in kg/m^2).

2.6. Statistical analysis

All statistical analysis were performed in the statistical software environment R (R Core Team, 2017). Response variables were SOC stocks, C/N ratio, the isotopic ratios of organic carbon $\alpha^{13}C/^{12}C$ and organic nitrogen $\alpha^{15}N/^{14}N$, as well as, their enrichment factors. All response variables were checked for normality and where necessary, log-transformation was applied (SOC stocks and C/N ratios were log-transformed, whereas the isotopic ratios were left untransformed). The selection of the variables was based on a principal component analysis (PCA, R-packages *"prcomp"* and *"factoextra"*, (Kassambara and Mundt, 2017)). Two analyses of variance (ANOVA) were tested for each horizon / fraction: the first one consisted only of the response variable and the first three principal components (PCs) and the second one consisted of the first PC (PC1) and the categorical variables 'climate', 'region', and 'forest type'. In the ANOVA analyses, the function aov.ko was used with *keep.order* option set true to prevent reordering of independent variables in the model. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity. Results with a p-value < 0.05 were considered significant, results with $0.05 < p < 0.1$ as marginally significant. Data throughout the paper is expressed as means ± standard errors.

3. RESULTS

3.1. Soil and site characteristics

3.1.1. Climate, forest type, and soil chemistry

The sampling sites have a MAT ranging from 1.1 to 11.8°C and a MAP from 704 to 2216 mm. There were 28 sites covered by broadleaf trees and 26 coniferous sites. Values of pH varied between 3.1 and 7.6, whereas values of exchangeable contents of Fe and Al (at soil depth 0-20 cm) were ranging between 0 and 2.2 mmolc/kg and 0 and 38.1 mmolc/kg, respectively.

3.1.2. PCA components

The PCA extracted three components, explaining 72% of the total variance (*Table 1*). PC1 was characterized with high loadings of soil physicochemical parameters, whereas PC2 was driven by MAT (0.63), PET (0.60), and broadleaf percentage (0.45). Finally, MAP was the single most important PC3 (-0.79).

Table 1. Results from the PCA analysis. The three most important principal components (PCs) presented below (values in bold show the values of the variables with the highest loadings).

PC components / **Parameters**	PC1	PC2	PC3
Al content	**-0.48**	0.11	0.17
Fe content	**-0.42**	0.02	0.33
Ca content	**0.42**	-0.10	0.23
pH	**0.45**	-0.04	0.11
Clay content	0.37	0.01	0.12
Broadleaf percentage	0.21	**0.45**	-0.38
MAT	-0.01	**0.63**	0.06
MAP	-0.15	-0.09	**-0.79**
PET	0.02	**0.60**	0.09
Importance of the components			
Standard deviation	1.8	1.5	1.1
Proportion of Variance	0.36	0.24	0.12
Cumulative Proportion	0.36	0.60	0.72

3.2. SOC stocks

3.2.1. Organic layer

The contribution of total POM (the sum of L, F, H horizons and fLF and oLF) to total SOM was highest in the warm-moist climatic conditions (72.3%, see *Fig. 3*). The contribution of the organic layer (L-F-H) relative to total SOC stocks was highest in cold-dry climates (nearly 40%), which was the climate condition with the smallest total SOC stocks (9.4 kg m^{-2}). In general, regardless of climatic condition, total POM contribution was always higher than MOM contribution (*Supplementary table 2*).

With respect to the organic layer, PC1 was highly significant only in the L horizon (SS=18%, *Table 2*). Furthermore, the second ANOVA test including PC1, climate, region, and forest type, showed a significant effect of the variable climate on SOC stocks in the L horizon (*p=0.02, SS=10.9%*). PC2 revealed no significance in any of the examined fractions.

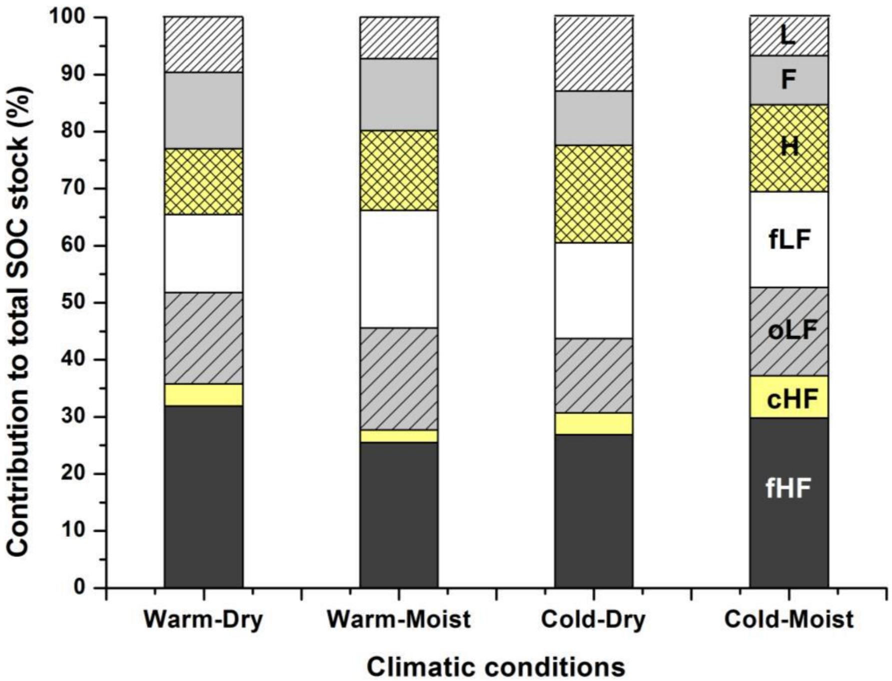

Fig. 3: Contribution of fractions to total SOC stocks according to climatic conditions.

Table 2. Results ANOVA analysis for SOC stocks. Two analyses were performed for each horizon/fraction: one with the three PCs (1), and another with PC1 and the categorical variables climate, region, and forest type (2). The sign "#" indicates that the variable was not included in the model. Sum of squares (SS) are shown in percentages; F represents the F-values. Degrees of freedom are shown in parenthesis after the F values (first value shows the degrees of freedom of the individual variable, the second one - the total degrees of freedom of the model). R^2 indicates adjusted R^2 (total explained model variance) and is shown in bold.

Explanatory variables / Response variables			PC1 (soil chemistry)	PC2 (MAT + forest type)	PC3 (MAP)	Climate	Region	Forest type	Residual **(R^2)**
SOC stocks all	(1)	SS	2.1	0.1	0.3	#	#	#	97.5
		F	$F_{(1, 417)}$=8.8 **	$F_{(1,417)}$=0.4 n. s.	$F_{(1, 417)}$=0.4 n. s.	#	#	#	**0.02**
	(2)	SS	2.1	#	#	0.2	0.6	0.2	96.9
		F	$F_{(1,411)}$=8.8 *	#	#	$F_{(3,411)}$=0.3 n. s.	$F_{(4,411)}$=0.7 n. s.	$F_{(1,411)}$=0.4 n. s.	**0.01**
	(1)	SS	18.0	0.4	1.3	#	#	#	80.3
		F	$F_{(1,64)}$=14.4 ***	$F_{(1,64)}$=0.3 n. s.	$F_{(1,64)}$=1.0 n. s.	#	#	#	**0.16**

L	(2)	SS	18.0	#	#	10.9	5.6	2.6	62.9
		F	$F_{(1,58)}=16.6$ ***	#	#	$F_{(3,58)}=0.02$ *	$F_{(4,58)}=1.3$ n. s.	$F_{(1,58)}=2.4$ n. s.	**0.27**
F	(1)	SS	6.4	8.2	0.9	#	#	#	84.5
		F	$F_{(1,27)}=2.0$ n. s.	$F_{(1,27)}=2.6$ n. s.	$F_{(1,27)}=0.3$ n. s.	#	#	#	**0.06**
	(2)	SS	6.4	#	#	20.2	8.7	0.5	64.2
		F	$F_{(1,21)}=2.0$ n. s.	#	#	$F_{(3,21)}=2.0$ n. s.	$F_{(4,21)}=2.0$ n. s.	$F_{(1,21)}=2.0$ n. s.	**0.08**
H	(1)	SS	10.2	5.5	0.3	#	#	#	84.0
		F	$F_{(1,17)}=2.1$ n. s.	$F_{(1,17)}=1.1$ n. s.	$F_{(1,17)}=0.1$ n. s.	#	#	#	**0.01**
	(2)	SS	10.2	#	#	7.0	19.8	6.5	56.5
		F	$F_{(1,11)}=1.9$ n. s.	#	#	$F_{(3,11)}=0.5$ n. s.	$F_{(4,11)}=0.9$ n. s.	$F_{(1,11)}=1.3$ n. s.	**0**
fLF	(1)	SS	0.7	1.0	0.2	#	#	#	98.1
		F	$F_{(1,50)}=0.4$ n. s.	$F_{(1,50)}=0.5$ n. s.	$F_{(1,50)}=0.1$ n. s.	#	#	#	**0**
	(2)	SS	0.7	#	#	4.9	9.0	2.4	83.0
		F	$F_{(1,44)}=0.4$ n. s.	#	#	$F_{(3,44)}=0.9$ n. s.	$F_{(4,44)}=1.2$ n. s.	$F_{(1,44)}=1.3$ n. s.	**0**
oLF	(1)	SS	4.2	0.7	3.4	#	#	#	91.7
		F	$F_{(1,50)}=2.3$ n. s.	$F_{(1,50)}=0.4$ n. s.	$F_{(1,50)}=1.8$ n. s.	#	#	#	**0.03**
	(2)	SS	4.2	#	#	2.2	6.3	0.4	86.9
		F	$F_{(1,44)}=2.1$ n. s.	#	#	$F_{(3,44)}=0.4$ n. s.	$F_{(4,44)}=0.8$ n. s.	$F_{(1,44)}=0.2$ n. s.	**0**
cHF	(1)	SS	26.4	1.5	4.9	#	#	#	67.2
		F	$F_{(1,50)}=19.6$ ***	$F_{(1,50)}=1.1$ n. s.	$F_{(1,50)}=3.6$.	#	#	#	**0.29**
	(2)	SS	26.4	#	#	9.2	3.4	0.02	60.98
		F	$F_{(1,44)}=19.1$ ***	#	#	$F_{(3,44)}=2.2$ n. s.	$F_{(4,44)}=0.6$ n. s.	$F_{(1,44)}=0.01$ n. s.	**0.27**
fHF	(1)	SS	0.3	3.7	4.3	#	#	#	91.7
		F	$F_{(1,50)}=0.1$ n. s.	$F_{(1,50)}=2.0$ n. s.	$F_{(1,50)}=2.3$ n. s.	#	#	#	**0.03**
	(2)	SS	0.3	#	#	4.4	14.2	1.1	80.0
		F	$F_{(1,44)}=0.1$ n. s.	#	#	$F_{(3,44)}=0.8$ n. s.	$F_{(4,44)}=1.9$ n. s.	$F_{(1,44)}=0.6$ n. s.	**0.04**

3.2.2. Mineral soils 0-20 and 0-120 cm

The contribution of the MOM was greatest in cold-moist climates, whereas the contribution of total POM to total SOC was smallest (62.8%). Within the two HFs, fHF had a higher contribution than cHF (*Fig. 3*). PC1 had a significant impact on the cHF fraction (SS=26.4%, *Table 2*). PC2 revealed no significance in any of the examined fractions. The MAP-driven PC3 had a marginal effect on SOC stocks in the cHF fraction (*p=0.06, SS=4.9%*). In the additional analysis of the corresponding SOC stocks in the mineral soil at 0-120 cm soil depth, PC3 had the highest explanatory power (SS=20.6%, *Supplementary table 3a*). Extrapolating the analysis to a Swiss-wide dataset (n=842), we observed the same effect of PC3, though the component explained a little less from the model variance (SS=20%, see *Supplementary table 3b*).

3.3. Soil fractionation

C/N ratios differed according to fractions and decreased in the following order: root (35.1±1.4) > L (25.8±0.6) > oLF (25.8±0.8) > fLF (23.9±0.7) > F (23.4±0.6) > H (21.2±0.9) > cHF (16.3±0.4) > fHF (12.3±0.3). Furthermore, ratios did not differ among different climatic conditions, except for the H horizon and the deep mineral soil (*Fig. 4*). The H horizon demonstrated lower C/N ratios in warmer conditions (18.4±0.3 and 16.7±0.5 in warm-moist and warm-dry climates, respectively) as compared to those in cold climates (22.4±1.3 and 23.8±2.5, for cold-moist and cold-dry, respectively). In the corresponding mineral soil (0-120 cm soil depth), the C/N ratio in the cold-moist climate was higher than the remaining climates (19.5±5.7 vs. 17.6±2.4, 15.4±1.4, 14.8±0.8 for warm-dry, warm-moist, and cold-dry, respectively).

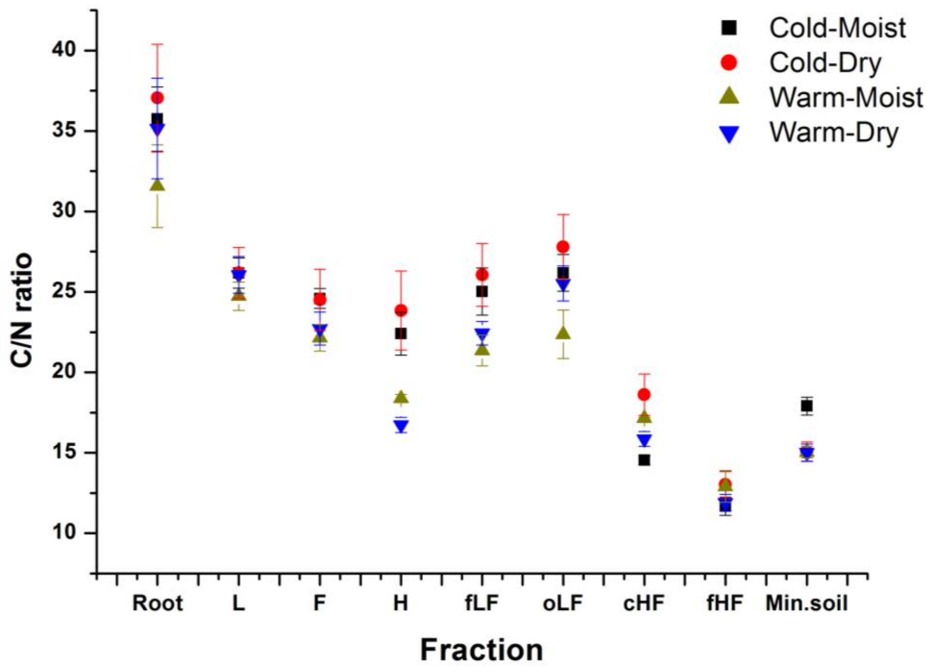

Fig. 4. Distribution of C/N ratios according to fractions and climatic conditions.

The values of $\delta^{13}C$ increased (became less negative) in the following order: L < Root < F < H < fLF = oLF < cHF < fHF (*Supplementary figs. 1 and 2*). The two light fractions demonstrated almost identical values (-27.5‰±0.1 and -27.5‰±0.2 for fLF and oLF, respectively), whereas the horizons in the organic layer as well as the two heavy fractions demonstrated an enrichment in $\delta^{13}C$ of over 1‰ (*Supplementary table 1*). We observed a total enrichment in $\delta^{15}N$ of 6‰ from the L horizon to the fHF. $\delta^{15}N$ values in the horizons of the organic layer were similar in magnitude (approx. -4.5‰). The POM $\delta^{15}N$ values of the light fractions were also similar (-2.1‰), whereas cHF and fHF differed (*Supplementary table 1*). Furthermore, when comparing $\delta^{15}N$ values according to the four climatic conditions, the highest $\delta^{15}N$ for all fractions (except for fHF) was found under the climate cold-dry (*Fig. 5*).

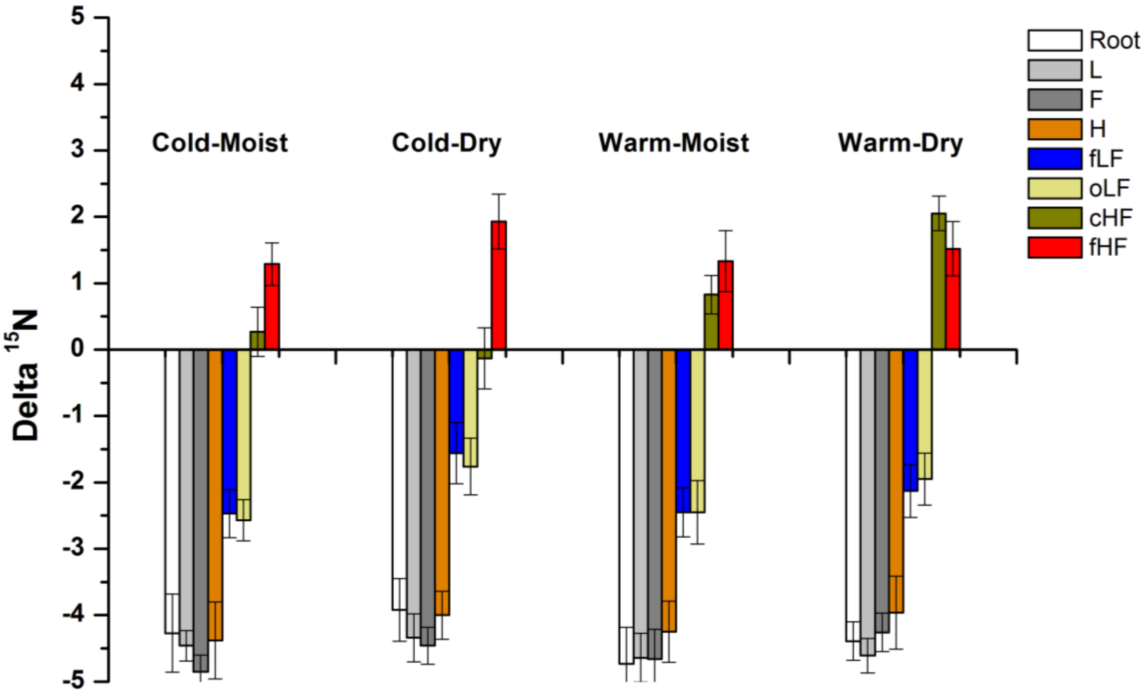

Fig. 5. Effect of climate on the isotopic ratios of $\delta^{15}N$ values for the organic layer, POM, and MOM. Data presented as means ± standard errors.

Furthermore, $\delta^{15}N$ values decreased relative to C/N ratios in the following order: fHF < cHF < fLF < oLF < roots, whereas the three organic layer horizons (L-F-H) showed different ranges (*Fig. 6*). The roots demonstrated lower $\delta^{15}N$ values in conifer trees as compared to broadleaf ones (-4.61±0.3 vs. -3.9±0.4). The same trend but to a lesser degree was observed in the L and F horizons and the two light fractions (*Fig. 6*).

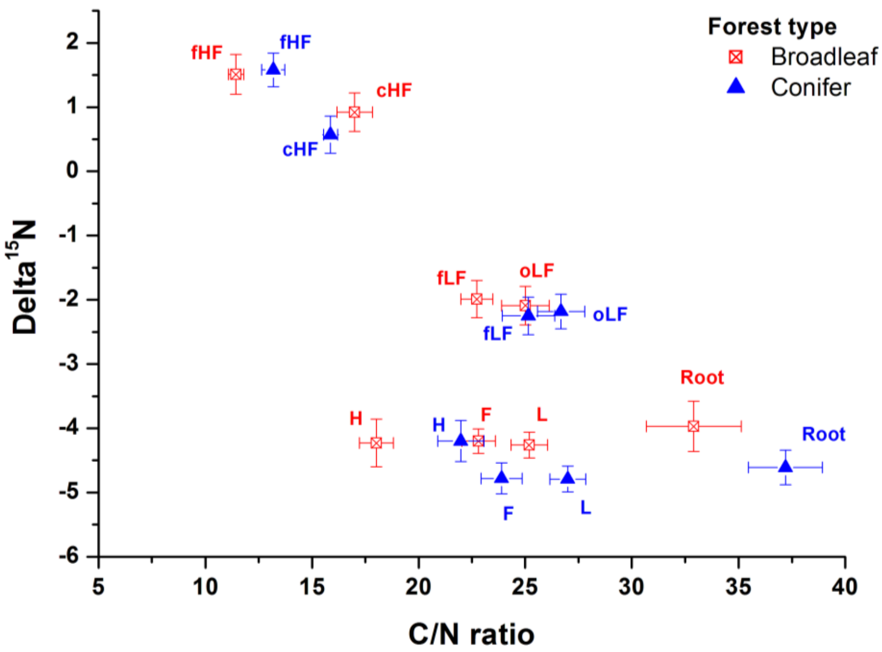

Fig. 6. Isotopic ratio of δ15N vs. C/N ratio according to fractions and forest type based on the concept for stabilization of SOM by Conen et al., (2008).

The MAT and forest type-driven PC2 demonstrated a significant impact on C/N ratios in the H horizon as well as on the organic layer roots and the fLF and fHF fractions (*Table 3*). In particular in the H horizon, PC2 explained a large part of the model variation (SS = 55.1%). The impact of climate on the H horizon was also confirmed by the second ANOVA test, however, the variance explained by it was smaller (SS = 43.1%) than in the first model including only the PCs. Though only demonstrating a marginal effect, climate explained a large part of the variance (SS = 35.4%) of C/N ratios in the cHF fraction and it further had a significant effect on C/N ratios in the fHF (SS = 9.2%). PC1 seemed to not be of importance for C/N ratios in any of the horizons / fractions but in the fHF, whereas the MAP-driven PC3 showed marginal significant effects on the L horizon and the oLF fraction. However, PC1 was the most important explanatory variable for C/N ratios in the mineral soils (0-120 cm), explaining more from the model variance (SS = 9.3%) than PC2 and PC3 together (*Supplementary table 3*). Furthermore, C/N ratios seem to differ regionally, as the variable region had a significant impact on the L and F horizons, the roots, and the oLF and fHF fractions.

Table 3. Results ANOVA analysis for C/N and the δ15N isotopic ratio. Two analyses were performed for each horizon/fraction: one with the three PCs (1), and another with PC1 and the categorical variables climate, region, and forest type (2). The sign "#" indicates that the variable was not included in the model. Sum of squares (SS) are shown in percentages; F represents the F-values. Degrees of freedom are shown in parenthesis after the F values (first value shows the degrees of freedom of the individual variable, the

second one - the total degrees of freedom of the model). R^2 indicates adjusted R^2 (total explained model variance) and is shown in bold.

Response variable			PC1	PC2	PC3	Climate	Region	Forest type	Residual (**R^2**)
C/N ratio									
L	(1)	SS	0.0	1.8	4.5	#	#	#	93.7
		F	$F_{(1,59)}=0.0$ n. s.	$F_{(1,59)}=1.1$ n. s.	$F_{(1,59)}=2.8$.	#	#	#	**0.02**
	(2)	SS	0.0	#	#	1.8	19.6	1.0	77.6
		F	$F_{(1,53)}=0.0$ n. s.	#	#	$F_{(3,53)}=0.4$ n. s.	$F_{(4,53)}=3.3$ *	$F_{(1,53)}=0.7$ n. s.	**0.09**
F	(1)	SS	1.3	6.6	2.7	#	#	#	89.4
		F	$F_{(1,28)}=0.4$ n. s.	$F_{(1,28)}=2.1$ n. s.	$F_{(1,28)}=0.8$ n. s.	#	#	#	**0.01**
	(2)	SS	1.3	#	#	8.4	48.6	1.4	40.3
		F	$F_{(1,22)}=0.7$ n. s.	#	#	$F_{(3,22)}=1.5$ n. s.	$F_{(4,22)}=6.6$ **	$F_{(1,22)}=0.8$ n. s.	**0.43**
H	(1)	SS	0.0	55.1	0.0	#	#	#	44.9
		F	$F_{(1,16)}=0.0$ n. s.	$F_{(1,16)}=19.7$ ***	$F_{(1,16)}=0.0$ n. s.	#	#	#	**0.47**
	(2)	SS	0.0	#	#	43.1	17.6	2.2	37.1
		F	$F_{(1,10)}=0.0$ n. s.	#	#	$F_{(3,10)}=3.9$ *	$F_{(4,10)}=1.2$ n. s.	$F_{(1,10)}=0.6$ n. s.	**0.29**
Roots	(1)	SS	0.2	15.2	2.9	#	#	#	81.7
		F	$F_{(1,40)}=0.1$ n. s.	$F_{(1,40)}=7.5$ **	$F_{(1,40)}=1.4$ n. s.	#	#	#	**0.12**
	(2)	SS	0.2	#	#	5.0	19.3	2.8	72.7
		F	$F_{(1,34)}=0.1$ n. s.	#	#	$F_{(3,34)}=0.8$ n. s.	$F_{(4,34)}=2.2$.	$F_{(1,34)}=1.3$ n. s.	**0.08**
fLF	(1)	SS	0.7	14.4	1.7	#	#	#	83.2
		F	$F_{(1,48)}=0.4$ n. s.	$F_{(1,48)}=8.3$ ***	$F_{(1,48)}=1.0$ n. s.	#	#	#	**0.03**
	(2)	SS	0.7	#	#	9.5	12.8	2.7	74.3
		F	$F_{(1,42)}=0.4$ n. s.	#	#	$F_{(3,42)}=1.8$ n. s.	$F_{(4,42)}=1.8$ n. s.	$F_{(1,42)}=1.5$ n. s.	**0.10**
oLF	(1)	SS	0.0	6.7	3.1	#	#	#	90.2
		F	$F_{(1,50)}=0.0$ n. s.	$F_{(1,50)}=3.7$ n. s.	$F_{(1,50)}=1.7$.	#	#	#	**0.04**
	(2)	SS	0.0	#	#	9.9	21.4	1.0	67.7
		F	$F_{(1,44)}=0.0$ n. s.	#	#	$F_{(3,44)}=2.1$ n. s.	$F_{(4,44)}=3.5$ *	$F_{(1,44)}=0.7$ n. s.	**0.18**
cHF	(1)	SS	2.6	0.0	6.3	#	#	#	91.1
		F	$F_{(1,12)}=0.3$ n. s.	$F_{(1,12)}=0.0$ n. s.	$F_{(1,12)}=0.8$ n. s.	#	#	#	**0**
	(2)	SS	2.6	#	#	35.4	40.3	0.8	20.9
		F	$F_{(1,6)}=0.8$ n. s.	#	#	$F_{(3,6)}=3.4$.	$F_{(4,6)}=2.9$ n. s.	$F_{(1,6)}=0.2$ n. s.	**0.48**
fHF	(1)	SS	33.4	6.2	0.3	#	#	#	60.1
		F	$F_{(1,49)}=27.2$ ***	$F_{(1,49)}=5.1$ *	$F_{(1,49)}=0.2$ n. s.	#	#	#	**0.36**
	(2)	SS	33.4	#	#	9.2	14.0	1.7	41.7
		F	$F_{(1,43)}=34.4$ ***	#	#	$F_{(3,43)}=3.2$ *	$F_{(4,43)}=3.6$ *	$F_{(1,43)}=1.7$ n. s.	**0.49**
$\delta^{15}N$									
L	(1)	SS	1.4	0.1	5.7	#	#	#	92.8
		F	$F_{(1,59)}=0.9$ n. s.	$F_{(1,59)}=0.1$ n. s.	$F_{(1,59)}=3.6$.	#	#	#	**0.03**
	(2)	SS	1.4	#	#	0.9	21.7	2.4	73.6
		F	$F_{(1,53)}=1.0$ n. s.	#	#	$F_{(3,53)}=0.2$ n. s.	$F_{(4,53)}=0.2$ **	$F_{(1,53)}=1.8$ n. s.	**0.14**

F	(1)	SS	1.7	15.4	13.4	#	#	#	69.5
		F	$F_{(1,28)}=0.7$ n. s.	$F_{(1,28)}=6.2$ *	$F_{(1,28)}=5.4$ *	#	#	#	0.23
	(2)	SS	1.7	#	#	6.7	25.4	3.4	62.8
		F	$F_{(1,22)}=0.6$ n. s.	#	#	$F_{(3,22)}=0.8$ n. s.	$F_{(4,22)}=2.2$.	$F_{(1,22)}=1.2$ n. s.	**0.12**
H	(1)	SS	0.2	0.0	0.2	#	#	#	99.6
		F	$F_{(1,16)}=0.0$ n. s.	$F_{(1,16)}=0.0$ n. s.	$F_{(1,16)}=0.0$ n. s.	#	#	#	**0**
	(2)	SS	0.2	#	#	1.9	45.2	3.6	49.1
		F	$F_{(1,10)}=0.0$ n. s.	#	#	$F_{(3,10)}=0.1$ n. s.	$F_{(4,10)}=2.3$ n. s.	$F_{(1,10)}=0.7$ n. s.	**0.06**
Root	(1)	SS	0.6	3.2	0.0	#	#	#	96.2
		F	$F_{(1,40)}=0.2$ n. s.	$F_{(1,40)}=1.3$ n. s.	$F_{(1,40)}=0.0$ n. s.	#	#	#	**0**
	(2)	SS	0.6	#	#	3.7	7.0	8.4	80.3
		F	$F_{(1,34)}=0.2$ n. s.	#	#	$F_{(3,34)}=0.5$ n. s.	$F_{(4,34)}=0.7$ n. s.	$F_{(1,34)}=3.5$.	**0**
fLF	(1)	SS	0.3	0.1	1.3	#	#	#	98.3
		F	$F_{(1,49)}=0.1$ n. s.	$F_{(1,49)}=0.0$ n. s.	$F_{(1,49)}=0.6$ n. s.	#	#	#	**0**
	(2)	SS	0.3	#	#	6.6	15.4	1.5	76.2
		F	$F_{(1,43)}=0.2$ n. s.	#	#	$F_{(3,43)}=1.2$ n. s.	$F_{(4,43)}=2.2$.	$F_{(1,43)}=0.8$ n. s.	**0.08**
oLF	(1)	SS	2.0	0.1	0.1	#	#	#	97.8
		F	$F_{(1,50)}=1.0$ n. s.	$F_{(1,50)}=0.1$ n. s.	$F_{(1,50)}=0.1$ n. s.	#	#	#	**0**
	(2)	SS	2.0	#	#	7.1	15.1	0.4	75.4
		F	$F_{(1,44)}=1.1$ n. s.	#	#	$F_{(3,44)}=1.4$ n. s.	$F_{(4,44)}=2.2$.	$F_{(1,44)}=0.3$ n. s.	**0.09**
cHF	(1)	SS	23.4	3.6	2.9	#	#	#	70.1
		F	$F_{(1,10)}=3.3$.	$F_{(1,10)}=0.5$ n. s.	$F_{(1,10)}=0.4$ n. s.	#	#	#	**0.09**
	(2)	SS	23.4	#	#	34.8	17.4	4.5	19.9
		F	$F_{(1,4)}=4.7$.	#	#	$F_{(3,4)}=2.3$ n. s.	$F_{(4,4)}=0.9$ n. s.	$F_{(1,4)}=0.9$ n. s.	**0.35**
fHF	(1)	SS	6.8	0.4	0.1	#	#	#	92.7
		F	$F_{(1,49)}=3.6$.	$F_{(1,49)}=0.2$ n. s.	$F_{(1,49)}=0.0$ n. s.	#	#	#	**0.02**
	(2)	SS	6.8	#	#	5.7	4.8	0.8	81.9
		F	$F_{(1,43)}=3.6$.	#	#	$F_{(3,43)}=1.0$ n. s.	$F_{(4,43)}=0.6$ n. s.	$F_{(1,43)}=0.4$ n. s.	**0.01**

PC1, associated with high loadings of soil chemistry, had a marginal effect on $\delta^{15}N$ in the two heavy fractions (SS = 23.4% and SS = 6.8%, for cHF and fHF, respectively). Furthermore, $\delta^{15}N$ ratios in the L and F horizons were affected by PC3 whereas PC2 had a significant effect on the F horizon but not on the L (*Table 3*). The soil chemical PC1 was only of importance in $\delta^{13}C$ values in the L horizon and the oLF fraction (*Supplementary table 4*), whereas the variance explained by the climate-driven PC2 was higher in the two light fractions and the H horizon. The ANOVA analyses revealed that for the enrichment factor of $\delta^{13}C$, PC2 exerted a marginally significant effect (*p=0.06, Supplementary table 5*). The enrichment factor of $\delta^{15}N$ was influenced by the soil chemical PC1 and the MAP-driven PC3 (SS = 9.4% and SS = 4.1%, respectively). Furthermore, values of the ^{13}C enrichment factor became more negative from cold to warm climates, whereas the highest values for the enrichment factor of ^{15}N were observed in warm-moist climates and the lowest were detected in cold-moist ones (*Fig. 7*).

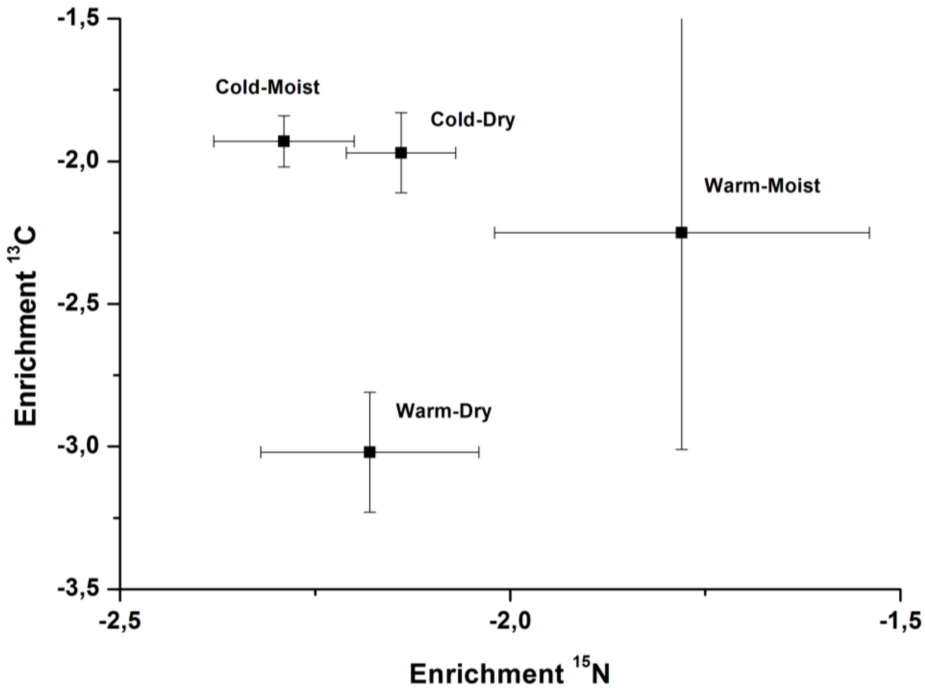

Fig. 7. Enrichment ^{13}C factor vs. enrichment ^{15}N factor according to the four climatic conditions.

4. DISCUSSION

In our study investigating SOC stocks and SOM pool distribution along natural environmental gradients with different geochemical and climatic conditions, climate had a rather negligible effect on SOC stocks and composition, whereas the effect of soil chemistry was more dominant. Furthermore, the chemical characteristics of SOM pools separated according to their density organic matter strongly suggest that mineral associated OM in the uppermost 20 cm of soils primarily derives from roots and not from the organic layer. Both MOM quantity and quality was not related to climatic conditions.

The density fractionation clearly separated SOM pools with distinct physical and chemical characteristics (Schrumpf et al., 2013; Griepentrog et al., 2014). The strong decrease in C/N ratios and an enrichment in ^{15}N from the free light fractions to the mineral-associated ‘heavy’ fractions indicates an increasing contribution of microbial residues during SOC transformation (Conen et al., 2008). Against our hypothesis that SOM quality but not SOC stocks would depend on climate, there was no consistent effect of temperature and moisture on the pool distribution and the characteristics within the pools. The highest contribution of POM to total SOC stocks was found in warm-moist climatic conditions (> 72%, see *Fig. 3, Supplementary table 2*) whereas the lowest one was found in cold-moist climates (62.8%). Moreover, the PCA components representing climate were not significantly related to the pool distribution. These findings are apparently in contradiction to an alpine grassland study in Switzerland by (Leifeld et al., 2009), which reported an increasing POM to total SOM contribution with an increasing elevation (corresponding to colder climates). One explanation could be the smaller span in climatic conditions in our study with the highest forested site at 1885 m a.s.l.. It could also be related to the broader spectra of physicochemical conditions in our study, which superimposed an apparently small effect by climatic conditions. Our findings, however, are consistent with the study by Doetterl et al., (2015) along large environmental gradients in South America that precipitation and temperature were only secondary predictors for carbon storage, respiration, residence time and stabilization mechanisms. Although climate did not seem to be primarily related to SOM, it could exert an indirect influence by an enhanced weathering in warmer and moister soils. For instance, soils of Southern Switzerland with the highest MAP and MAT have also particularly high contents of SOM stabilizing Fe- and Al-oxides (Eckmeier et al., 2010). In our study however we cannot disentangle the indirect effect of climate from a direct geochemical one.

Overall, the forest soils analyzed in this study had substantially greater contributions in POM than grassland soils. While in the forested soils, the contribution of POM to total SOM was on average 65% with half of it being stored in the organic layer, studies in grasslands have found POM contributions of about 30% in the same depth interval (Leifeld et al., 2009). Other studies have observed significantly greater amounts of POM in subalpine forests than in grasslands (Kayler et al., 2011; Poeplau and Don, 2013). Likely explanation for the greater accumulation of POM in forests could be smaller inputs from roots in forests than in grassland (Solly et al., 2013), an input of more recalcitrant litter and a smaller bioturbation in forests (Mills et al., 2013). Greater amounts of POM makes forested soils potentially more vulnerable to disturbances than grassland soils.

Among SOM fractions, C/N ratios decreased in the following order: root < L < oLF < fLF < F < H < cHF < fHF, indicating an advanced SOM decomposition towards mineral associated SOM. Similar results were also found by Gunina and Kuzyakov, (2014) and by Schrumpf et al., (2013). C/N ratios are generally lower in more stable OM compounds, indicating a greater breakdown of SOM (Batjes, 1996). Simultaneously, isotopic ratios of $\delta^{15}N$ become more enriched (Kramer et al., 2003), very likely reflecting the accumulation of microbial residues. An increase in OM stability is associated with the relation between a decreasing C/N ratio and increasing $\delta^{15}N$ values (Conen et al., 2008). The same significant pattern was observed in this study (*Fig. 6*), with $\delta^{15}N$ increasing with decreasing C/N ratio from roots > occluded and free LF > cHF > fHF, reflecting a preferential loss of lighter N during microbial decomposition and an accumulation of microbial residues with a small C/N ratio during SOM transformation (Conen et al., 2008). In contrast to roots, the L-F-H horizons do not fit in the observed pattern. Although there is an increase in $\delta^{15}N$ values towards the light fraction, C/N ratio remained constant, strongly suggesting that C and N are lost at the same rate and hence there is no accumulation of microbial residues with a smaller C/N ratio (*Fig. 6*). In turn, this pattern indicates the organic layer did hardly contribute to SOC in the heavy mineral associated fractions.

The effect of climate on C/N ratios was not univocal and differed according to fractions. PC2 (temperature- and forest-type-driven) was the most important explanatory variable in the fLF fraction, the H horizon, and the organic layer roots, whereas PC3 affected C/N ratios in the L horizon and the oLF fraction. Although there are studies demonstrating that C/N ratios in European forest soils are forest-type dependent in top soils (Cools et al., 2014), the ANOVA tests did not reveal a strong effect of forest type (*Table 3*). Since soil mineral properties can affect also tree species (Boca and Van Miegroet, 2017), we assume that a possible tree species effect in our study might have been overridden by the effects of soil chemistry. Such a trend has been observed in an Aspen-conifer montane forests in Utah, USA (Román Dobarco and Van Miegroet, 2014).

Surprisingly, climate did not have a stronger effect on SOC stocks in the organic layer and the light fractions as compared to the heavy ones (considered better stabilized). Our results are in agreement with recent studies such as the study by Schnecker et al., (2016), who found no effect on SOM pools after 7 years of forest soil warming. Furthermore, in an elevational gradient study in the Tibetan Plateau, Wang et al., (2015) found no effect of temperature on SOM decomposition. Along a temperate forest altitudinal gradient, Tian et al., (2016) discovered that through the effect on soil texture and nitrogen availability, MAT is only an indirect measure for SOM stability. Nonetheless, the MAP-driven PC3 demonstrated a significant effect on SOC stocks in the deep mineral soil (*Supplementary table 3*). These results corroborate results from an earlier study of these forest sites (Gosheva et al., 2017), which found MAP to exert a strong positive effect on mineral soil SOC stocks. Though climate itself indicated no significant impact on the $\delta^{15}N$ values (except for in the F horizon), a stronger ^{15}N enrichment was observed in warm climates, as compared to cold ones (*Fig. 7*). Since temperature enhances microbial activity, which promotes mineralization and nitrification processes, climate could have had an indirect effect on $\delta^{15}N$ values in this study. Furthermore, the soil chemistry PC1 was found to be more important for the two heavy fractions, which could be associated with the chemical composition of litter input (Tamura et al., 2017) likely resulting from shifting vegetation cover along an elevational gradient, but could also be related to differences in soil pathways based on soil texture. Our results corroborate a global study of Craine et al., (2015), which found climate to be only an indirect intermediary of $\delta^{15}N$. In our study, the two light and two heavy fractions were more enriched in $\delta^{15}N$ under warm-dry as compared to cold-moist climatic conditions, which was also similar to what was found by Craine et al., (2015). Generally, $\delta^{15}N$ values increase with soil depth (since N concentration decreases), leading to a higher amount of more stable OM with soil depth (Piccolo et al., 1996). Since soil chemistry exerts a strong effect on C and N in deeper soil depths, the increase in the $\delta^{15}N$ values might be either a result of a ^{14}N depletion during nitrification or due to enrichment of SOM in $\delta^{15}N$ by stabilization through mineral association. SOC in mineral-associated fractions is more difficult to decompose compared to particulate OC (Vesterdal et al., 2011), since SOM is better stabilized (Liao et al., 2006; Conen et al., 2008). In our study, we found soil chemistry to be more important for the mineral-associated OM than the particulate one (*Table 3*). This highlights the importance of interactions with minerals and is in agreement with other studies (Schrumpf et al., 2013; Tian et al., 2016). In this study, the means of $\delta^{13}C$ and $\delta^{15}N$ were very similar for fLF and oLF (*Supplementary table 1*), preventing a conclusion which fraction is better stabilized. Similar challenges have been observed by other studies (e.g. Schrumpf et al., (2013)), referring to the methodology of density fractionation as a possible obstacle.

In our study, $\delta^{13}C$ values in fHF increased by 1‰ relative to cHF and by 1.3‰ relative to the light fractions (*Supplementary table 1*), which further increased by 1.4‰ relative to the L horizon in the organic layer (therefore, a total enrichment of 2.7‰ between MOM fraction and the organic layer). Usually, a certain quantity of $\delta^{13}C$ increase with soil depth can be expected due to the decrease of atmospheric $\delta^{13}C$ (Francey et al., 1999). However, a 2‰ change is also possible independent of a $\delta^{13}C$ decrease of atmospheric CO_2 (Torn et al., 2002; Boström et al., 2007). This offers a further possible explanation that the observed total increase of 2.7‰ may have occurred because of $\delta^{13}C$ enrichment during humification, but is not conclusive. A further explanation may be based on other mechanisms, such as preferential decomposition of ^{13}C depleted components or sorption of dissolved OC holding different isotopic values (Torn et al., 1997).

The signals of $\delta^{13}C$ in SOC are related to land use history (Giardina and Ryan, 2000) and to litter quality (Wang et al., 2015). From a previous study of the sites (Gosheva et al., 2017), it is known that the majority of the examined sites had been afforested at least 120 years ago. Mixing different qualities of C (forest-derived and e.g. grassland-derived C) could also lead to changes in the isotopic ratios as some other studies have shown (Boström et al., 2007; Hiltbrunner et al., 2013). Therefore, due to changes in land-use and alterations in climatic conditions, predominantly predicted for higher elevations (Hagedorn et al., 2010), we could expect variations in the isotopic signal of OC, resulting in changes in SOM pool distribution.

5. CONCLUSION

Our study based on 54 sites along large environmental gradients in Swiss forests indicate a minor direct effect of climate. MAP affected significantly SOC stocks in the deeper mineral soils (0-120 cm soil depth), but not in the topsoil or the organic layer. In contrast, physicochemical properties exerted a more dominant effect than climate, in particular. An increase in ^{15}N from the organic layer to the light and heavy fraction in the mineral soil but unchanged C/N ratio strongly suggest that organic layer does not contribute to SOC in the heavy fractions. This suggests that above-ground litter inputs make only a small contribution to long-term C sequestration.

6. ACKNOWLEDGEMENTS

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7. REFERENCES

Batjes, N.H., 1996. Total carbon and nitrogen in the soils of the world. Eur. J. Soil Sci. 151–163.

Bellamy, P.H., Loveland, P.J., Bradley, R.I., Lark, R.M., Kirk, G.J.D., 2005. Carbon losses from all soils across England and Wales 1978-2003. Nature 437, 245–248. doi:10.1038/nature04038

Blume, H.-P., Brümmer, G.W., Fleige, H., Horn, R., Kandeler, E., Kögel-Knabner, I., Kretzschmar, R., Stahr, K., Wilke, B.-M., 2016. Scheffer/SchachtschabelSoil Science. Springer Berlin Heidelberg, Berlin, Heidelberg. doi:10.1007/978-3-642-30942-7

Boca, A., Van Miegroet, H., 2017. Can Carbon Fluxes Explain Differences in Soil Organic Carbon Storage under Aspen and Conifer Forest Overstories? Forests 8, 118. doi:10.3390/f8040118

Boström, B., Comstedt, D., Ekblad, A., 2007. Isotope fractionation and 13C enrichment in soil profiles during the decomposition of soil organic matter. Oecologia 153, 89–98. doi:10.1007/s00442-007-0700-8

Bradford, M.A., Wieder, W.R., Bonan, G.B., Fierer, N., Raymond, P.A., Crowther, T.W., 2016. Managing uncertainty in soil carbon feedbacks to climate change. Nat. Clim. Change 6, 751–758. doi:10.1038/nclimate3071

Braun-Blanquet, J., 1964. Pflanzensoziologie. Springer Vienna, Vienna. doi:10.1007/978-3-7091-8110-2

Cerli, C., Celi, L., Kalbitz, K., Guggenberger, G., Kaiser, K., 2012. Separation of light and heavy organic matter fractions in soil ? Testing for proper density cut-off and dispersion level. Geoderma 170, 403–416. doi:10.1016/j.geoderma.2011.10.009

Conen, F., Zimmermann, M., Leifeld, J., Seth, B., Alewell, C., 2008. Relative stability of soil carbon revealed by shifts in delta 15N and C:N ratio. Biogeosciences 5, 123–128.

Cools, N., Vesterdal, L., De Vos, B., Vanguelova, E., Hansen, K., 2014. Tree species is the major factor explaining C:N ratios in European forest soils. For. Ecol. Manag. 311, 3–16. doi:10.1016/j.foreco.2013.06.047

Craine, J.M., Elmore, A.J., Wang, L., Augusto, L., Baisden, W.T., Brookshire, E.N.J., Cramer, M.D., Hasselquist, N.J., Hobbie, E.A., Kahmen, A., Koba, K., Kranabetter, J.M., Mack, M.C., Marin-Spiotta, E., Mayor, J.R., McLauchlan, K.K., Michelsen, A., Nardoto, G.B., Oliveira, R.S., Perakis, S.S., Peri, P.L., Quesada, C.A., Richter, A., Schipper, L.A., Stevenson, B.A., Turner, B.L., Viani, R.A.G., Wanek, W., Zeller, B., 2015. Convergence of soil nitrogen isotopes across global climate gradients. Sci. Rep. 5. doi:10.1038/srep08280

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173. doi:10.1038/nature04514

Doetterl, S., Stevens, A., Six, J., Merckx, R., Van Oost, K., Casanova Pinto, M., Casanova-Katny, A., Muñoz, C., Boudin, M., Zagal Venegas, E., Boeckx, P., 2015. Soil carbon storage controlled by interactions between geochemistry and climate. Nat. Geosci. 8, 780–783. doi:10.1038/ngeo2516

Eckmeier, E., Egli, M., Schmidt, M.W.I., Schlumpf, N., Nötzli, M., Minikus-Stary, N., Hagedorn, F., 2010. Preservation of fire-derived carbon compounds and sorptive stabilisation promote the accumulation of organic matter in black soils of the Southern Alps. Geoderma 159, 147–155. doi:10.1016/j.geoderma.2010.07.006

Francey, R.J., Allison, C.E., Etheridge, D.M., Trudinger, C.M., Enting, I.G., Leuenberger, M., Langenfelds, R.L., Michel, E., Steele, L.P., 1999. A 1000-year high precision record of δ13C in atmospheric CO2. Tellus B 51, 170–193.

Garten Jr, C.T., 2004. Soil carbon dynamics along an elevation gradient in the southern Appalachian mountains. ORNL.

Gee, G.W., Bauder, J.W., 1986. Particle-size analysis, in: Methods of Soil Analysis. pp. 383–411.

Giardina, C.P., Ryan, M.G., 2000. Evidence that decomposition rates of organic carbon inmineral soil do not vary with temperature. Nature.

Gnägi, C., Labhart, T., 2015. Geologie der Schweiz. hep-verlag, Bern.

Gonseth, Y., Wohlgemuth, T., Sansonnens, B., Buttler, A., 2001. Die biogeographischen Regionen der Schweiz. Erläuterungen und Einteilungsstandard. (No. Umwelt Materialien Nr. 137). Bundesamt für Umwelt, Wald und Landschaft, Bern.

González Domínguez, B.R.G., Niklaus, P.A., Studer, M.S., Hagedorn, F., Wacker, L., Haghipour, N., Climate influence on SOC dynamics overridden by soil and landform properties. *In prep.*

Gosheva, S., Walthert, L., Niklaus, P.A., Zimmermann, S., Gimmi, U., Hagedorn, F., 2017. Reconstruction of Historic Forest Cover Changes Indicates Minor Effects on Carbon Stocks in Swiss Forest Soils. Ecosystems. doi:10.1007/s10021-017-0129-9

Griepentrog, M., Bodé, S., Boeckx, P., Hagedorn, F., Heim, A., Schmidt, M.W.I., 2014. Nitrogen deposition promotes the production of new fungal residues but retards the decomposition of old residues in forest soil fractions. Glob. Change Biol. 20, 327–340. doi:10.1111/gcb.12374

Gunina, A., Kuzyakov, Y., 2014. Pathways of litter C by formation of aggregates and SOM density fractions: Implications from 13C natural abundance. Soil Biol. Biochem. 71, 95–104. doi:10.1016/j.soilbio.2014.01.011

Hagedorn, F., Mulder, J., Jandl, R., 2010. Mountain soils under a changing climate and land-use. Biogeochemistry 97, 1–5. doi:10.1007/s10533-009-9386-9

Hiltbrunner, D., Zimmermann, S., Hagedorn, F., 2013. Afforestation with Norway spruce on a subalpine pasture alters carbon dynamics but only moderately affects soil carbon storage. Biogeochemistry 115, 251–266. doi:10.1007/s10533-013-9832-6

Hoyle, F.C., O?Leary, R.A., Murphy, D.V., 2016. Spatially governed climate factors dominate management in determining the quantity and distribution of soil organic carbon in dryland agricultural systems. Sci. Rep. 6. doi:10.1038/srep31468

Kassambara, A., Mundt, F., 2017. factoextra: Extract and Visualize the Results of Multivariate Data.

Kayler, Z.E., Kaiser, M., Gessler, A., Ellerbrock, R.H., Sommer, M., 2011. Application of δ^{13}C and δ^{15}N isotopic signatures of organic matter fractions sequentially separated from adjacent arable and forest soils to identify carbon stabilization mechanisms. Biogeosciences 8, 2895–2906. doi:10.5194/bg-8-2895-2011

Kramer, M.G., Sollins, P., Sletten, R.S., Swart, P.K., 2003. N isotope fractionation and measures of organic matter alteration during decomposition. Ecology 84, 2021–2025.

Lal, R., 2005. Forest soils and carbon sequestration. For. Ecol. Manag. 220, 242–258. doi:10.1016/j.foreco.2005.08.015

Leifeld, J., Zimmermann, M., Fuhrer, J., Conen, F., 2009. Storage and turnover of carbon in grassland soils along an elevation gradient in the Swiss Alps. Glob. Change Biol. 15, 668–679. doi:10.1111/j.1365-2486.2008.01782.x

Liao, J.D., Boutton, T.W., Jastrow, J.D., 2006. Organic matter turnover in soil physical fractions following woody plant invasion of grassland: Evidence from natural 13C and 15N. Soil Biol. Biochem. 38, 3197–3210. doi:10.1016/j.soilbio.2006.04.004

Lorenz, K., Lal, R., 2010. Carbon Sequestration in Forest Ecosystems. Springer Netherlands, Dordrecht. doi:10.1007/978-90-481-3266-9

Mills, R.T.E., Tipping, E., Bryant, C.L., Emmett, B.A., 2013. Long-term organic carbon turnover rates in natural and semi-natural topsoils. Biogeochemistry 118, 257–272. doi:10.1007/s10533-013-9928-z

Piccolo, M.C., Neill, C., Melillo, J.M., Cerri, C.C., Steudler, P.A., 1996. 15N natural abundance in forest and pasture soils of the Brazilian Amazon Basin. Plant Soil 249–258.

Poeplau, C., Don, A., 2013. Sensitivity of soil organic carbon stocks and fractions to different land-use changes across Europe. Geoderma 192, 189–201. doi:10.1016/j.geoderma.2012.08.003

R Core Team, 2017. R: A language and environment for statistical computing R Foundation for Statistical Computing.

Román Dobarco, M., Van Miegroet, H., 2014. Soil Organic Carbon Storage and Stability in the Aspen-Conifer Ecotone in Montane Forests in Utah State, USA. Forests 5, 666–688. doi:10.3390/f5040666

Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., K?gel-Knabner, I., Lehmann, J., Manning, D.A.C., Nannipieri, P., Rasse, D.P., Weiner, S., Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. Nature 478, 49–56. doi:10.1038/nature10386

Schnecker, J., Borken, W., Schindlbacher, A., Wanek, W., 2016. Little effects on soil organic matter chemistry of density fractions after seven years of forest soil warming. Soil Biol. Biochem. 103, 300–307. doi:10.1016/j.soilbio.2016.09.003

Schrumpf, M., Kaiser, K., Guggenberger, G., Persson, T., K?gel-Knabner, I., Schulze, E.-D., 2013. Storage and stability of organic carbon in soils as related to depth, occlusion within aggregates, and attachment to minerals. Biogeosciences 10, 1675–1691. doi:10.5194/bg-10-1675-2013

Six, J., Conant, R.T., Paul, E.A., Paustian, K., 2002. Stabilization mechanisms of soil organic matter: Implications for C-saturation of soils. Plant Soil 155–176.

Sjögersten, S., Alewell, C., Cécillon, L., Hagedorn, F., Jandl, R., Leifeld, J., Martinsen, V., Schindlbacher, A., Sebastià, M.-T., Van Miegroet, H., 2011. Mountain Soils in a Changing Climate – Vulnerability of Carbon Stocks and Ecosystem Feedbacks, in: Soil Carbon in Sensitive European Ecosystems: From Science to Land Management. John Wiley & Sons, Ltd, Chichester, UK.

Smith, P., 2008. Land use change and soil organic carbon dynamics. Nutr. Cycl. Agroecosystems 81, 169–178. doi:10.1007/s10705-007-9138-y

Solly, E., Sch?ning, I., Boch, S., M?ller, J., Socher, S.A., Trumbore, S.E., Schrumpf, M., 2013. Mean age of carbon in fine roots from temperate forests and grasslands with different management. Biogeosciences 10, 4833–4843. doi:10.5194/bg-10-4833-2013

Song, B., Niu, S., Zhang, Z., Yang, H., Li, L., Wan, S., 2012. Light and Heavy Fractions of Soil Organic Matter in Response to Climate Warming and Increased Precipitation in a Temperate Steppe. PLoS ONE 7, e33217. doi:10.1371/journal.pone.0033217

Tamura, M., Suseela, V., Simpson, M., Powell, B., Tharayil, N., 2017. Plant litter chemistry alters the content and composition of organic carbon associated with soil mineral and aggregate fractions in invaded ecosystems. Glob. Change Biol. doi:10.1111/gcb.13751

Tian, Q., He, H., Cheng, W., Bai, Z., Wang, Y., Zhang, X., 2016. Factors controlling soil organic carbon stability along a temperate forest altitudinal gradient. Sci. Rep. 6. doi:10.1038/srep18783

Torn, M.S., Swanston, C.W., Castanha, C., Trumbore, S.E., 2009. Storage and turnover of organic matter in soils, in: Biophysico-Chemical Processes Involving Natural Nonliving

Organic Matter in Environmental Systems. JohnWiley & Sons, Inc., Hoboken, NJ, USA, pp. 215–268.

Torn, M.S., Lapenis, A.G., Timofeev, A., Fischer, M.L., Babikov, B.V., Harden, J.W., 2002. Organic carbon and carbon isotopes in modern and 100-year-old-soil archives of the Russian steppe. Glob. Change Biol. 8, 941–953.

Torn, M.S., Trumbore, S.E., Chadwick, O.A., Vitousek, P.M., Hendricks, D.M., 1997. Mineral control of soil organic carbon storage and turnover. Nature 389.

Vesterdal, L., Leifeld, J., Poeplau, C., Don, A., van Wesemael, B., 2011. Land-use change effects on soil carbon stocks in temperate regions – development of carbon response functions, in: Soil Carbon in Sensitive European Ecosystems: From Science to Land Management. John Wiley & Sons.

von Lützow, M., Kögel-Knabner, I., Ekschmitt, K., Flessa, H., Guggenberger, G., Matzner, E., Marschner, B., 2007. SOM fractionation methods: Relevance to functional pools and to stabilization mechanisms. Soil Biol. Biochem. 39, 2183–2207. doi:10.1016/j.soilbio.2007.03.007

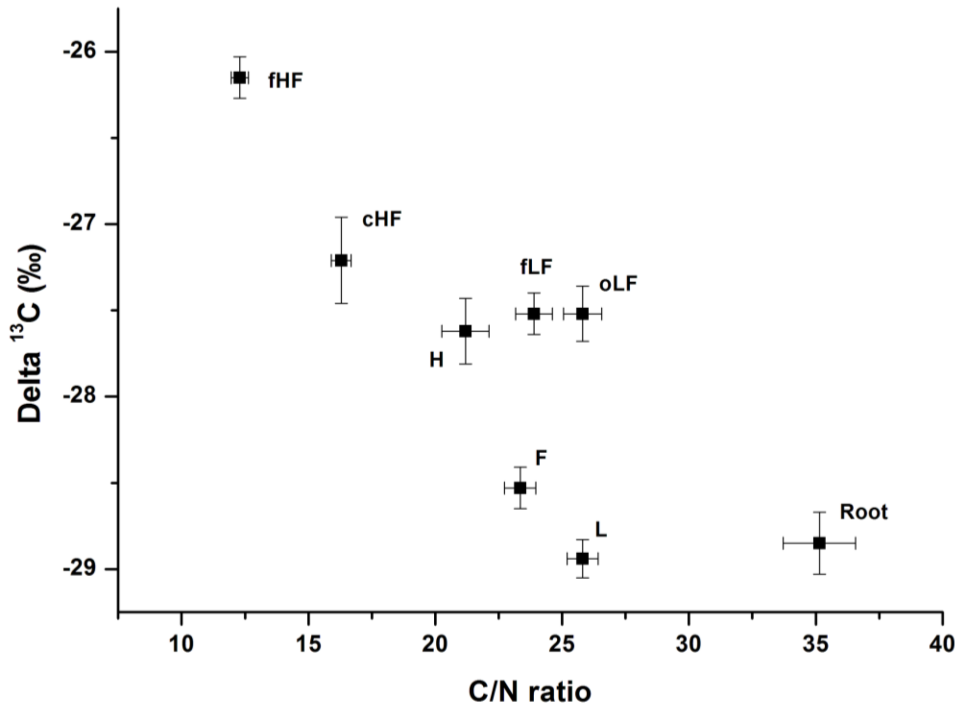
Walthert, L., Graf, U., Kammer, A., Luster, J., Pezzotta, D., Zimmermann, S., Hagedorn, F., 2010. Determination of organic and inorganic carbon, ? ^{13} C, and nitrogen in soils containing carbonates after acid fumigation with HCl. J. Plant Nutr. Soil Sci. 173, 207–216. doi:10.1002/jpln.200900158

Wang, G., Jia, Y., Li, W., 2015. Effects of environmental and biotic factors on carbon isotopic fractionation during decomposition of soil organic matter. Sci. Rep. 5. doi:10.1038/srep11043

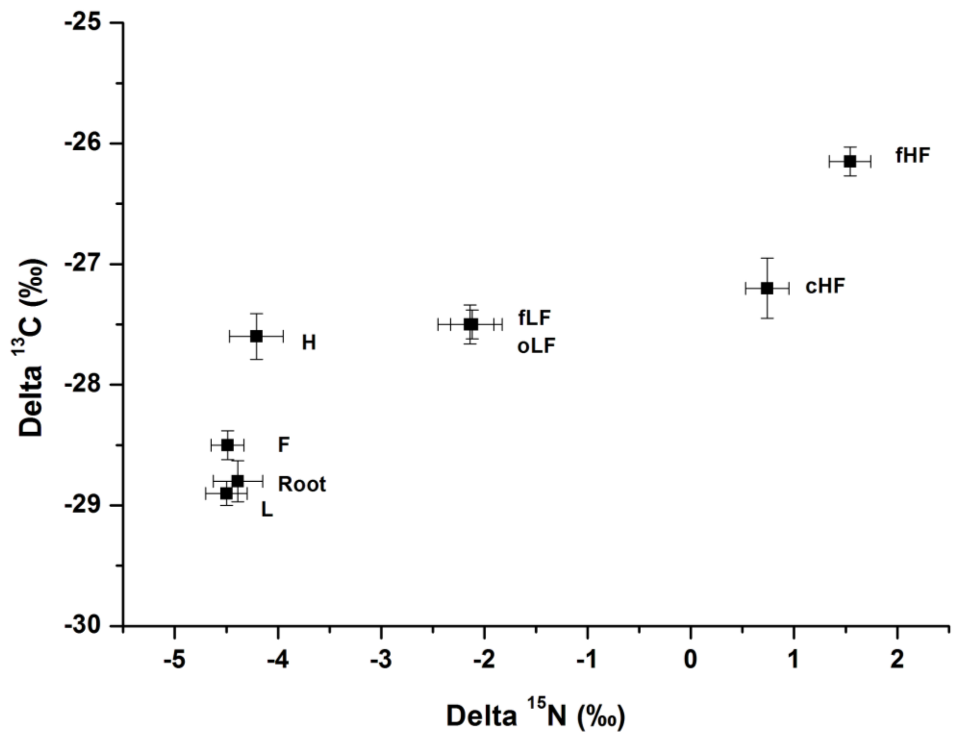
Wiesmeier, M., Prietzel, J., Barthold, F., Spörlein, P., Geuß, U., Hangen, E., Reischl, A., Schilling, B., von Lützow, M., Kögel-Knabner, I., 2013. Storage and drivers of organic carbon in forest soils of southeast Germany (Bavaria) ? Implications for carbon sequestration. For. Ecol. Manag. 295, 162–172. doi:10.1016/j.foreco.2013.01.025

8. APPENDIX

Supplementary figure 1. δ^{13}C ratios vs. C/N ratios of the fractions.



Supplementary figure 2. Isotopic ratios (δ^{13}C vs. δ^{15}N) according to fractions.



Supplementary table 1. Mean values of ratios according to fractions.

	C/N	$\delta^{13}C$	$\delta^{15}N$
Root	35.1±1.4	-28.9±0.2	-4.3±0.2
L	25.8±0.6	-28.9±0.1	-4.5±0.1
F	23.4±0.6	-28.5±0.1	-4.5±0.2
H	21.2±0.9	-27.6±0.2	-4.2±0.3
fLF	23.9±0.7	-27.5±0.1	-2.1±0.2
oLF	25.8±0.8	-27.5±0.2	-2.1±0.2
cHF	16.3±0.4	-27.2±0.3	0.7±0.2
fHF	12.3±0.3	-26.2±0.1	1.5±0.2

***Supplementary table 2*:** Contributions of the individual fractions (in %) for SOC stocks according to climatic conditions.

Climate / **Contribution (%)**	Warm-Dry	Warm-Moist	Cold-Dry	Cold-Moist
L to total SOC	9.7	7.2	12.9	6.7
F to total SOC	13.4	12.6	9.5	8.6
H to total SOC	11.5	14.0	17.1	15.2
Org. layer to total SOC	***34.6***	***33.8***	***39.5***	***30.5***
fLF to total SOC	13.7	20.6	16.8	16.8
oLF to total SOC	16.0	17.9	13.0	15.5
Total POM* to total SOC	***64.2***	***72.3***	***69.3***	***62.8***
cHF to total SOC	3.9	2.2	3.8	7.4
fHF to total SOC	31.9	25.5	26.9	29.8
Total MOM to total SOC	***35.8***	***27.7***	***30.7***	***37.2***
Total SOC stocks (in kg C m^{-2})	10.4	14.1	9.4	10.5

* Total POM is the sum of the L-F-H horizons from the organic layer and the two light fractions.

The sum of total POM and total MOM equals 100%.

Supplementary table 3. Summary results from ANOVA tests for a.) corresponding SOC stocks and C/N ratios at soil depth 0-120 cm, and b.) extrapolated from a bigger Swiss-wide soil dataset (n=842). The sign "#" indicates that the variable was not included in the model. Sum of squares (SS) are shown in percentages; F represents the F-values. Degrees of freedom are shown in parenthesis after the F values (first value shows the degrees of freedom of the individual variable, the second one - the total degrees of freedom of the model). R^2 indicates adjusted R^2 (total explained model variance) and is shown in bold.

Response variables \ Explanatory variables			PC1	PC2	PC3	Climate	Region	Forest type	Residual **(R^2)**
a.) Corresponding SOC stocks and C/N ratios at soil depth 0-120 cm (n=47)									
SOC stocks	(1)	SS	2.1	0.1	20.6	#	#	#	77.2
		F	$F_{(1,41)}$=1.1 n. s.	$F_{(1, 41)}$=0.1 n. s.	$F_{(1, 41)}$=10.9 **	#	#	#	**0.17**
	(2)	SS	2.1	#	#	0.5	20.5	0.7	76.2
		F	$F_{(1,35)}$=0.9 n. s.	#	#	$F_{(3,35)}$=0.1 n. s.	$F_{(4,35)}$=2.4 .	$F_{(1,35)}$=0.3 n. s.	**0.04**
C/N ratio	(1)	SS	8.2	13.5	2.2	#	#	#	76.1
		F	$F_{(1,41)}$= 0.04 *	$F_{(1,41)}$= 0.01 *	$F_{(1,41)}$=0.3 n. s.	#	#	#	**0.18**
	(2)	SS	8.2	#	#	3.9	8.3	0.5	79.1
		F	$F_{(1,35)}$=3.7 .	#	#	$F_{(3,35)}$=0.6 n. s.	$F_{(4,35)}$=0.9 n. s.	$F_{(1,35)}$=0.2 n. s.	**0.01**
b.) Swiss-wide soil dataset (n=842)									
SOC stocks	(1)	SS	0.5	0.1	20.0	#	#	#	79.4
		F	$F_{(1,839)}$=5.1 *	$F_{(1,839)}$=0.9 n. s.	$F_{(1,839)}$=211.6 ***	#	#	#	**0.20**
	(2)	SS	0.5	#	#	3.6	8.3	0.3	87.3
		F	$F_{(1,831)}$=4.7 *	#	#	$F_{(3,831)}$=11.4 ***	$F_{(4,831)}$=19.8 ***	$F_{(1,831)}$=2.9 .	**0.12**
C/N ratio	(1)	SS	9.3	0.6	4.6	#	#	#	85.5
		F	$F_{(1,839)}$=90.7 ***	$F_{(1,839)}$=5.7 *	$F_{(1,839)}$=44.6 ***	#	#	#	**0.14**
	(2)	SS	9.3	#	#	4.9	3.0	0.1	82.7
		F	$F_{(1,831)}$=93.1 ***	#	#	$F_{(3,831)}$=16.6 ***	$F_{(4,831)}$=7.5 ***	$F_{(1,831)}$=0.9 n.s.	**0.16**

Supplementary table 4. Summary results from ANOVA tests for δ^{13}C from the 54 site dataset. The sign "#" indicates that the variable was not included in the model. Sum of squares (SS) are shown in percentages; F represents the F-values. Degrees of freedom are shown in parenthesis after the F values (first value shows the degrees of freedom of the individual variable, the second one - the total degrees of freedom of the model). R^2 indicates adjusted R^2 (total explained model variance) and is shown in bold.

Response variables \ Explanatory variables			PC1	PC2	PC3	Climate	Region	Forest type	Residual **(R^2)**
δ^{13}C									
L	(1)	SS	4.2	15.4	0.1	#	#	#	80.3
		F	$F_{(1,59)}=3.1$.	$F_{(1,59)}=11.4$ **	$F_{(1,59)}=0.1$ n. s.	#	#	#	**0.16**
	(2)	SS	4.2	#	#	20.2	7.4	3.9	64.3
		F	$F_{(1,53)}=3.5$.	#	#	$F_{(3,53)}=5.5$ **	$F_{(4,53)}=1.5$ n. s.	$F_{(1,53)}=3.2$.	**0.25**
F	(1)	SS	0.1	50.8	0.0	#	#	#	49.1
		F	$F_{(1,28)}=0.1$ n. s.	$F_{(1,28)}=28.9$ n. s.	$F_{(1,28)}=0.0$ n. s.	#	#	#	**0.46**
	(2)	SS	0.1	#	#	17.4	13.0	21.3	48.2
		F	$F_{(1,22)}=0.1$ n. s.	#	#	$F_{(3,22)}=2.6$.	$F_{(4,22)}=1.5$ n. s.	$F_{(1,22)}=9.7$ ***	**0.32**
H	(1)	SS	0.0	62.1	1.8	#	#	#	36.1
		F	$F_{(1,16)}=0.0$ n. s.	$F_{(1,16)}=27.5$ ***	$F_{(1,16)}=0.8$ n. s.	#	#	#	**0.57**
	(2)	SS	0.0	#	#	50.2	9.0	23.4	17.4
		F	$F_{(1,10)}=0.0$ n. s.	#	#	$F_{(3,10)}=9.6$ **	$F_{(4,10)}=1.3$ n. s.	$F_{(1,10)}=13.5$ **	**0.83**
Root	(1)	SS	1.9	11.4	6.3	#	#	#	80.4
		F	$F_{(1,40)}=0.9$ n. s.	$F_{(1,40)}=5.7$ *	$F_{(1,40)}=3.2$.	#	#	#	**0.14**
	(2)	SS	1.9	#	#	22.2	7.2	0.5	68.2
		F	$F_{(1,34)}=0.9$ n. s.	#	#	$F_{(3,34)}=3.7$ *	$F_{(4,34)}=0.9$ n. s.	$F_{(1,34)}=0.2$ n. s.	**0.14**
fLF	(1)	SS	0.0	44.6	3.9	#	#	#	51.5
		F	$F_{(1,50)}=0.0$ n. s.	$F_{(1,50)}=43.3$ ***	$F_{(1,50)}=3.8$.	#	#	#	**0.45**
	(2)	SS	0.0	#	#	21.3	16.0	17.1	45.6
		F	$F_{(1,44)}=0.0$ n. s.	#	#	$F_{(3,44)}=6.9$ ***	$F_{(4,44)}=3.9$ **	$F_{(1,44)}=16.6$ ***	**0.45**
oLF	(1)	SS	6.0	23.0	5.9	#	#	#	65.1
		F	$F_{(1,50)}=4.6$ *	$F_{(1,50)}=17.7$ ***	$F_{(1,50)}=4.5$ *	#	#	#	**0.31**
	(2)	SS	6.0	#	#	11.3	14.6	14.4	53.7
		F	$F_{(1,44)}=4.9$ *	#	#	$F_{(3,44)}=3.1$ *	$F_{(4,44)}=2.9$ *	$F_{(1,44)}=11.8$ **	**0.35**
cHF	(1)	SS	1.4	3.0	2.2	#	#	#	93.4
		F	$F_{(1,38)}=0.6$ n. s.	$F_{(1,38)}=1.2$ n. s.	$F_{(1,38)}=0.9$ n. s.	#	#	#	**0**
	(2)	SS	1.4	#	#	6.3	14.4	2.4	75.5
		F	$F_{(1,32)}=0.6$ n. s.	#	#	$F_{(3,32)}=0.9$ n. s.	$F_{(4,32)}=1.5$ n. s.	$F_{(1,32)}=1.0$ n. s.	**0.03**
fHF	(1)	SS	2.6	13.9	1.7	#	#	#	81.8
		F	$F_{(1,49)}=1.5$ n. s.	$F_{(1,49)}=8.4$ **	$F_{(1,49)}=1.0$ n. s.	#	#	#	**0.13**
	(2)	SS	2.5	#	#	16.3	20.7	6.8	53.7
		F	$F_{(1,43)}=2.1$ n. s.	#	#	$F_{(3,43)}=4.3$ **	$F_{(4,43)}=4.1$ **	$F_{(1,43)}=5.4$ *	**0.35**

Supplementary table 5. Summary results from ANOVA tests for the enrichment factors of $\delta^{13}C$ and $\delta^{15}N$ from the 54 site dataset. The sign "#" indicates that the variable was not included in the model. Sum of squares (SS) are shown in percentages; F represents the F-values. Degrees of freedom are shown in parenthesis after the F values (first value shows the degrees of freedom of the individual variable, the second one - the total degrees of freedom of the model). R^2 indicates adjusted R^2 (total explained model variance) and is shown in bold.

Response variables \ Explanatory variables			PC1	PC2	PC3	Climate	Region	Forest type	Residual **(R^2)**
Enrichment factor $\delta^{13}C$	(1)	SS	0.6	3.5	0.8	#	#	#	95.1
		F	$F_{(1,100)}$=0.6 n. s.	$F_{(1,100)}$=3.7 .	$F_{(1,100)}$=6.9 n. s.	#	#	#	**0.02**
	(2)	SS	0.6	#	#	3.0	11.5	0.2	84.7
		F	$F_{(1,94)}$=0.7 n. s.	#	#	$F_{(3, 94)}$=1.1 n. s.	$F_{(4, 94)}$=3.2 *	$F_{(1, 94)}$=0.3 n. s.	**0.07**
Enrichment factor $\delta^{15}N$	(1)	SS	9.4	0.6	4.1	#	#	#	85.9
		F	$F_{(1,100)}$=10.9 **	$F_{(1,100)}$=0.7 n. s.	$F_{(1,100)}$=4.7 *	#	#	#	**0.14**
	(2)	SS	9.4	#	#	3.2	6.0	0.5	80.9
		F	$F_{(1,94)}$=10.9 **	#	#	$F_{(1,94)}$=1.2 n. s.	$F_{(1,94)}$=1.7 n. s.	$F_{(1,94)}$=0.6 n. s.	**0.11**

Paper III

Disentangling soil organic carbon drivers in forest soils: a model based analysis of the Swiss soil inventory

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ABSTRACT

Soil organic carbon (SOC) stocks are controlled by plant litter input, climatic conditions, soil properties and land use. The quantitative importance of these factors is, however, not well understood and hence, their implementation in soil C models difficult. We aimed at disentangling the various factors driving SOC storage in Swiss forest soils. Our main approach was to analyze the discrepancies between measured and simulated SOC stocks. The measured SOC stocks were located in permanent forests across large environmental gradients in Switzerland, whereas SOC stock simulations were done using the soil carbon model Yasso15 driven by climate and litter inputs derived from the national forest inventory. Our hypothesis was that soil properties known to control SOM stabilization but not implemented in the model are key determinants of SOC stocks and thus explain the discrepancy between modeled and measured SOC stocks.

Forest SOC stocks are greatest in Southern Switzerland (17.0 ±1.5 kg C m^{-2}). Exchangeable Fe and Ca were of key importance for total SOC stocks, followed by precipitation (MAP). Litter inputs had only a minor statistical relation with SOC storage, while forest type and mean annual temperature (MAT) were of primary importance for organic layer C stocks. Yasso15 estimated SOC stocks adequately for three out of five biogeographical regions with average residuals of one kg C m^{-2}. However, Yasso15 systematically underestimated SOC stocks in Jura and Southern Alps (ΔSOC=-4.1±0.6 and -9.9±1.5 kg C m^{-2}, respectively), which was most closely related to exchangeable Fe and Ca contents, hence, physicochemical properties determining SOM stabilization. Measured-simulated SOC stocks discrepancies existed to a lesser extent at high MAP and in waterlogged soils. Overall, our findings show that SOM stabilization plays a key role for SOM storage at the national scale, which is, so far, not adequately represented in Yasso15 and other belowground C models.

Keywords: carbon storage, soil organic matter, soil C model, forest soils, measured-simulated discrepancy SOC stocks, soil chemistry, SOM stabilization

1. INTRODUCTION

Soil organic matter (SOM) plays a key role for most soil functions. It is the largest C pool of terrestrial ecosystems and it affects nutrient cycling and pollutant dynamics. Soil organic matter consists of a continuum of compounds with different sources, degree of decomposition, and turnover rates resulting from interacting biological, chemical, and physical processes (Schmidt et al., 2011). The large spatial variability and the inherent complexity of SOM make it difficult to estimate C stocks and how these respond to environmental changes will affect SOM (Schrumpf et al., 2011). SOM storage depends on the C input into soils, its transformation and its stabilization. Experimental work using isotopic tracers, spectroscopic, and molecular-marker techniques indicates that the interaction of organic compounds with mineral surfaces are of primary importance for SOM stabilization and hence more important for the long-term accumulation of C in soils than C inputs from plant productivity (Hagedorn et al., 2003; Marschner et al., 2008; Schmidt et al., 2011). Iron and aluminum oxides with high surface areas and reactivity bind and protect SOM (Oades, 1988; Kaiser and Guggenberger, 2003; Dümig et al., 2014). The incorporation of the experimental findings into an accurate numerical model applicable at the regional scale is, however, still insufficient, probably due to the complexity of the soil system, the spatial heterogeneity, and the rather qualitative knowledge of the processes (Braakhekke et al., 2011; Schmidt et al., 2011; Lehmann and Kleber, 2015). Current soil carbon models thus simplify the processes assuming that SOM storage depends on the quantity and quality of litter inputs and the climatic conditions controlling decomposition and 'humification' of organic matter (RothC, (Coleman and Jenkinson, 2014); Century, (Parton et al., 2001); Yasso, (Tuomi et al., 2009; Repo et al., 2017)).

Recent studies across biomes in South America have shown that SOM storage and dynamics were primarily controlled by the stabilization of SOM in the mineral soil and hence by geochemistry, while precipitation and temperature were only secondary predictors of SOM dynamics (Doetterl et al., 2015). In contrast, for forest soils in Bavaria (Germany) spanning a large environmental gradient in the temperate zone, Wiesmeier et al., (2013) observed climate as the controlling parameter of SOC storage with greater stocks in cool, humid mountainous regions and smaller stocks in areas with higher temperatures. In a repeated soil survey in the Bavarian Alps, Prietzel et al., (2016) attributed SOM losses to changes in precipitation during the last decades. Associated with environmental conditions, tree species were also observed to control SOM storage, particularly the distribution between organic layer and mineral soil (Jandl et al., 2007; Vesterdal et al., 2013; Wiesmeier et al., 2013; Gosheva et al., 2017).

Countries, committed to the Kyoto protocol of the United Nations Framework Convention on Climate Change (UNFCCC), are required to report changes in SOC stocks in forests (*IPCC*, 2006b). Since, for most countries, no measurements for SOC stock changes exist, model simulations are used as an alternative to predict SOC sequestration and estimate changes in C dynamics (Didion et al., 2016). For Switzerland as in a few other European countries, greenhouse gas (GHG) reporting on forest soils is based on the soil C cycling model Yasso (Hernández et al., 2017). The model has been developed for soils of various ecosystems (Tuomi et al., 2009, 2011) and is driven by readily available forest inventory and climate data (Tuomi et al., 2009, 2011). Whereas applications of Yasso07 in Finland (Rantakari et al., 2012) and Sweden (Ortiz et al., 2013) showed a good agreement between simulated and measured SOC stocks in general, recent studies have revealed an underestimation of SOC stocks in Southern Finland (Lehtonen et al., 2016) and in Southern Sweden (Tupek et al., 2016). These discrepancies were attributed to soil texture and soil moisture (Finland) as well as to nutrient status. Furthermore, the model was found to underestimate stocks in Norway (Dalsgaard et al., 2016a) and Switzerland (cf. Didion and Thurig, (2016)) suggesting that other processes contribute to SOC storage as for instance SOM stabilization by the interaction with soil minerals or also due to bias in model parameters. However, the newest, improved model Yasso15 has been calibrated with more measurements of litter decomposition and SOC stock measurements than Yasso07 (Repo et al., 2017).

We aimed to identify the key drivers for SOC storage for Swiss forest soils and to test the litter decomposition model Yasso15 in predicting SOC storage for Swiss forests. The employed observational data set of 564 forest soil profiles contained extensive information on SOC stocks but also on climatic conditions, forest biomass, and physicochemical soil properties. These forest sites are situated along an elevational range from 327 to 2055 m, and they span a large gradient in climate, geochemistry and forest types. Our specific objectives were: 1) to identify the main environmental parameters that control the storage of SOC in forest soils by statistical analysis, 2) to compare measured SOC stocks with the outputs of the Yasso15 model using litter inputs derived from the National Forest Inventory (NFI) and climate data, and 3) to examine the discrepancy (residuals) between measured and simulated SOC stocks by linking them to a multitude of physical and chemical soil properties, forest stand characteristics as well as climatic parameters. Our hypothesis was that SOM stabilizing components largely explain the discrepancies between measured and modeled SOC stocks, which would imply that they are of key importance for SOC storage at the national scale.

2. MATERIALS AND METHODS

2.1. Study area and sampling sites

From a soil database encompassing approximately 1000 soil profiles, we selected 564 soil profiles *(Fig. 1)* that were located in forests older than 120 years (Gosheva et al., 2017). In combination with the typically small-scale, individual-tree based management interventions, this ensured that there have been only minimal disturbances in the forest cover. To obtain representative sites for the modelling, NFI sampling plots were selected falling (Brändli, 2010) within a radius of 5 km of a soil profile site. Each soil profile site was thus represented by on average 8 NFI sites (min=1 site; max=20 sites). Switzerland is divided into five major biogeographic regions (*Fig. 1*) with specific bedrock and forest type composition. The majority of our sites are found in the Swiss Plateau (n=205), a region characterized mostly by more or less decalcified to still calcareous moraines and tertiary sediments (molasse). In the Pre-Alps, a region which consists mostly of decalcified to calcareous sediments (Gnägi and Labhart, 2015), we have selected 184 soil profiles. The remaining sites are in the Southern Alps (n=32) with mainly gneiss as bedrock, the Jura (n=57), dominated by limestone or marl, and the Alps (n=89) with heterogeneous bedrock (Gnägi and Labhart, 2015). Following the altitudinal differences, the highest fraction of conifer forests is in the Pre-Alps (38% of the area of the Pre-Alps), whereas the highest fraction of broadleaf tree species occurs in the Swiss Plateau (49%).

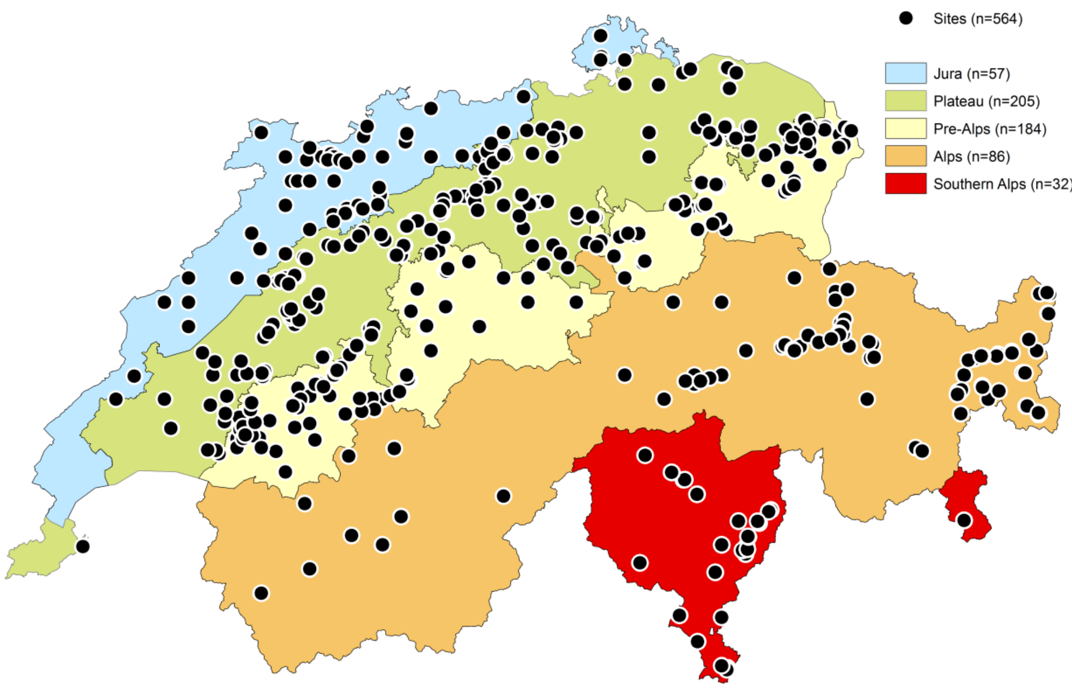

Fig. 1: Distribution of the forested soil sites in the five biogeographic regions of Switzerland. Note that the Alps with fewer sites are largely un-forested.

2.2. Soil, climate, and topography

Soil profiles were sampled by genetic horizons down to parent rock or to 120 cm soil depth when the parent rock was deeper. Composite soil samples were taken from the front wall of the soil profiles (over an average width of 70 cm). Samples were dried at 40-60°C and sieved with a 2 mm mesh for chemical analysis. Soil type was classified according to the World Reference Base from 2007 (WRB, 2007) and soils were grouped into three categories: waterlogged, acidic, and calcareous. Waterlogged soils (n=89) encompassed Gleysols and Stagnosols. After excluding waterlogged soils, calcareous (n=239) and acidic (n=236) soils were separated by the criterion whether lime was present in the fine earth fraction (< 2 mm) at a decalcified soil depth of one meter. Humus forms were classified into: mull (only L horizon present), moder (L + F horizons present), and mor (L, F and H horizons present). Soil texture was characterized by measuring the clay, silt and sand contents of 310 sites using the sedimentation method according to Gee and Bauder (1986). For the rest of the sites, we used field estimates based on ten soil texture classes (Walthert et al., 2004). Soil pH was measured in a 0.01 M $CaCl_2$ solution. Contents of the exchangeable Al, Fe, and Ca (in mmolc kg^{-1}) were obtained by 1 M ammonium chloride extraction (for details, see Walthert et al., (2004)). Soil properties were calculated for 0-30 cm and 0-100 cm depth intervals of the mineral soil by weighted averages of their contents according to the amount of fine earth in the various soil horizons.

Data on elevation and slope for all sites were determined from a 25-m digital elevation model (DEM, Swisstopo, (2011)). Additionally, some topographic parameters and exposition were assessed during the soil surveys. Exposition was categorized in the following groups: North, North-East, East, South-East, South, South-West, West, and North-West. Topography was grouped into four groups: flat area, foot slope, mid-slope, and summit. Annual climate data for each of the sites were obtained from the gridded data produced by the Swiss Federal Office of Meteorology and Climatology, MeteoSwiss (MeteoSwiss, 2013a,b). The data consisted of mean annual temperature, annual temperature amplitude, and mean annual precipitation (mean values for the time period 1961-1990). Finally, the Braun-Blanquet cover abundance scale (Braun-Blanquet, 1964) was used to quantify plant species in herb, shrub and tree layers. Percentage of broadleaved tree species was calculated as the sum of the cover of all broadleaf species divided by the sum of the cover of all tree species at canopy level. Forest was subdivided into two types based on the broadleaf percentage: coniferous (0-50%) and broadleaf (51-100%) forests.

2.3. Calculation of measured SOC stocks (based on the soil database)

SOC stocks were calculated separately for the organic layer (including L, F and H horizons) and the mineral soil at 0-100 cm soil depth. Total SOC stocks are represented by the sum of stocks in the organic layer and the mineral soil. SOC stocks in the organic layer were calculated according to Hagedorn et al., (2010a), with the mass of the organic layer calculated as the product of the density (L: 0.10 g/cm^3, F: 0.15 g/cm^3, H: 0.20 g/cm^3) and the volume (based on measured thickness), multiplied by its C content. Mineral soil SOC stocks were calculated using the following equation (*eq. 1*):

$$SOC_{hz} = \sum_i^z (h_i (1 - \theta_i) \rho_i C_i) \quad [eq. 1]$$

where SOC_{hz} represents SOC stocks of all horizons h_z (kg C m^{-2}), C_i - the carbon content of the horizon i (kg kg^{-1} of C), ρ_i is the density of the fine earth (g cm^{-3}), θ_i is the volumetric stone content (m^3 m^{-3}), and h_i is the horizon thickness (m). A pedotransfer function (PTF), based on a calibration dataset of 559 mineral soil horizons from 134 different sites and a validation set of 131 horizons from 34 sites, was used to estimate the fine earth density (Nussbaum et al., 2016). Covariates used in this PTF are sampling depth, slope, estimates of stone content and soil density, biogeographical unit, and C content. Total and organic C contents were measured in ground samples by dry combustion using an elemental analyzer (NC 2500, CE Instruments, Italy), with prior removal of inorganic C by use of HCl vapor of all samples with pH values higher than 6.0 (Walthert et al., 2010). In addition, SOC stocks were corrected for the slope by multiplying them with the cosine of the slope in order to adjust to the manner of collection of the soil profiles, which have been dug vertically irrespective of the slope.

2.4. Simulations of SOC stocks (Yasso15 model)

SOC stock simulations were conducted with the newest version of the soil carbon cycling model Yasso (Yasso15). The model was calibrated based on a global dataset of dead wood (Tuomi et al., 2011) and litter (Tuomi et al., 2009) decomposition studies, of soil carbon stocks and of soil chronosequences (Repo et al., 2017) making it potentially suitable for a wide range of environmental conditions. Based on data on litter inputs (i.e., dead wood, foliage etc.), Yasso simulates flows of C between four chemical classes of C compounds and a more recalcitrant humus ("H") pool as a function of temperature, temperature amplitude and precipitation. Litter inputs are thus sub-divided into the following four different chemical compounds: "A" stands for hydrolysable compounds in acid, "W" for compounds that are water soluble, "E" stands for compounds, which are ethanol soluble, and "N" for non-soluble compounds. Each of these compounds have different C decomposition rates and represent the group of labile fractions. The sum of the AWEN compound classes and the H pool equals total simulated SOC stocks, which are representative of SOC stored in mineral soils down to one meter soil depth, litter and dead wood.

The C stocks for the study sites were simulated following the protocol used for simulating C stocks and C stock changes for the Swiss Greenhouse Gas Inventory (Didion and Thurig, 2016; FOEN, 2017). Litter inputs were estimated separately for broadleaved and coniferous trees based on data from NFI sampling plots (Brändli, 2010) as functions of turnover rates for foliage and fine root (diameter (D) < ~5mm) litter and of tree growth, harvest and natural mortality for fine (D < ~7cm) and coarse (D ≥ ~7cm) woody debris including roots, twigs, branches and stems. Fine roots and foliage formed the group of non-woody litter, whereas the woody litter group consisted of twigs, coarse branches, stem wood, and coarse roots. C inputs for each pool were separated into the four chemical compartments following experimentally derived fractions as discussed in Didion et al., (2014). Data for observed climate were obtained for each simulated NFI plot from spatially gridded data prepared by the Federal Office of Meteorology and Climatology MeteoSwiss (see 2.2).

SOC stocks for the selected NFI plots within the 5 km radius of the soil measurements (cf. 2.1) were simulated as follows: (1) First, a spin-up simulation (cf. Liski et al., 2009) was conducted based on 30-year average climate (1961–1990) and constant C inputs from the first NFI (taking place from 1983-1985, (Swiss National Forest Inventory, 2017)) assuming that current SOC stocks have accumulated over centuries (cf. Gimmi et al., (2013)). (2) Then, simulation for 25 years with annual climate data for the period 1961 to 1985 and constant C inputs from the first NFI were run in order to cancel out the steady-state conditions after the spin-up phase (cf. Peltoniemi et al., (2007)). (3) Finally, simulations after 1986 based on plot-specific annual climate data and on carbon inputs derived for the three periods between two consecutive NFIs (i.e., NFI 1-2, NFI 2-3, and NFI 3-4, (Swiss National Forest Inventory, 2017)) were run.

2.5. Statistical analysis

Univariate analyses were performed to examine the main drivers of SOC storage. Carbon stocks in the organic layer, mineral soil and of the measured-modeled residuals were analyzed according to three steps. To summarize the rather large number of correlated explanatory variables, we first performed a principle component analysis (PCA) including the following numerical variables: slope, litter input, clay content, Fe-, Al-, and Ca- contents, MAT, and MAP. In a second step, the first three principal components (PCs), in combination with the categorical variables region, exposition, relief, and soil type, were examined in an analysis of variance (ANOVA) based on linear mixed effects models fitted by generalized least squares (gls, Pinheiro et al., (2017)). To account for the spatial autocorrelation of the residuals, an isotopic exponential decay of residual correlation with distance was fitted (*corExp(form=~ x+y),* where x and y are the Swiss grid coordinates of the sites. Finally, in order to identify the importance of individual variables on SOC stocks, an additional ANOVA test was performed, including the individual variables from the three PCs with the highest loadings. In the ANOVA, the function *aov.ko* was used with the option *keep.order = TRUE*, in order to prevent reordering of the independent variables. Measured SOC stocks were examined for the organic layer as well as total stocks (sum organic layer and mineral soil, soil depth 0-100 cm). SOC stock discrepancies were calculated as the difference between total measured and simulated SOC stocks. Analyses were performed for the entire dataset as well as divided into subsets (excluding waterlogged soils, excluding the region Southern Alps, sites with pH > 5 and pH < 5). Due to non-normality of the data, the numerical explanatory variables Fe, Ca, Al, pH, slope, litter input, clay content, MAT, and MAP, were log-transformed, whereas response variables (SOC stocks) were left untransformed. The normality of the residuals was tested with the Shapiro-Wilk normality test and by visualization using Q-Q plots. All data are reported as means ± standard error. All statistical analysis were performed in the statistical environment R 3.0.3 (R Core Team, 2017).

3. RESULTS

3.1. Site characteristics

Site properties were distinctly different among the five Swiss biogeographical regions (*Table 1*). Whereas soils in the Jura have highest contents of clay and Ca, the Southern Alps have the most acidic soils which have the highest contents of exchangeable Fe and Al. MAP was also highest in the Southern Alps and the Pre-Alps, whereas the Swiss Plateau had the highest MAT. In general, soils in conifer forests were more acidic and had higher contents of exchangeable Fe and Al than those in broadleaf forests (*data not shown*).

Table 1: Soil chemical parameters (pH and exchangeable contents of Fe, Al, and Ca), clay content down to 30 cm soil depth, and climate data in the five biogeographical regions of Switzerland (data presented as mean ± standard error).

Region / Soil parameters	***Jura (n=57)***	***Plateau (n=205)***	***Pre-Alps (n=184)***	***Alps (n=86)***	***Southern Alps (n=32)***	***Switzerland (n=564)***
Fe content (mmolc/kg)	0.2±0.1	0.5±0.1	0.9±0.1	0.6±0.1	1.3±0.3	0.7±0.1
Al content (mmolc/kg)	6.8±2.1	25.2±2.2	38.2±3.9	18.0±2.8	35.1±4.9	27.1±1.6
Ca content (mmolc/kg)	302.9±23.1	89.9±9.3	120.6±10.7	126.3±11.7	53.1±19.4	128.2±5.9
Clay content (%)	34.8±1.9	20.6±0.8	23.2±0.8	17.8±1.1	12.6±1.6	22.1±0.5
pH	6.3±0.2	4.9±0.1	4.9±0.1	5.3±0.2	4.3±0.2	5.0±0.06
MAT (°C)	7.9±0.2	8.4±0.1	6.7±0.1	3.3±0.3	7.0±0.4	6.8±0.1
MAP (mm)	1235.8±21.4	1188.4±13.6	1551.0±18.0	1078.1±29.2	1593.9±44.3	1325±11.9

The PCA extracted three principal components (PCs) that explained 67% of cumulative variance proportion (*Table 2*). PC1 was characterized by high loadings of soil chemical parameters: pH (0.47), Ca (0.46), Al (-0.43), and Fe (-0.40) explaining 35% of the variance proportion. PC2 was driven by MAT (-0.66), broadleaf percentage (-0.57), and slope (0.33), whereas PC3 had high loadings of MAP (0.67) and clay content (0.43, *Table 2*).

Table 2: Component matrix derived from the principal component analysis of 564 soil profiles. The bottom part shows results from ANOVA analyses of SOC stocks and the three components from the PCA analysis. The sign "-" indicates that the variable was omitted from the analysis due to insignificance, SS stands for sum of squares (in percentages), F stands for the F-value.

<table>
<tr><th colspan="2">PCA model</th><th colspan="2">PC 1</th><th colspan="2">PC 2</th><th colspan="2">PC 3</th></tr>
<tr><td colspan="2">Slope</td><td colspan="2">0.20</td><td colspan="2">0.33</td><td colspan="2">0.29</td></tr>
<tr><td colspan="2">Clay content</td><td colspan="2">0.34</td><td colspan="2">-0.09</td><td colspan="2">0.43</td></tr>
<tr><td colspan="2">Fe content</td><td colspan="2">-0.40</td><td colspan="2">0.09</td><td colspan="2">0.35</td></tr>
<tr><td colspan="2">Al content</td><td colspan="2">-0.43</td><td colspan="2">-0.06</td><td colspan="2">0.34</td></tr>
<tr><td colspan="2">Ca content</td><td colspan="2">0.46</td><td colspan="2">0.11</td><td colspan="2">0.23</td></tr>
<tr><td colspan="2">MAT</td><td colspan="2">0.09</td><td colspan="2">-0.66</td><td colspan="2">-0.006</td></tr>
<tr><td colspan="2">MAP</td><td colspan="2">-0.06</td><td colspan="2">-0.17</td><td colspan="2">0.67</td></tr>
<tr><td colspan="2">pH</td><td colspan="2">0.47</td><td colspan="2">0.12</td><td colspan="2">0.06</td></tr>
<tr><td colspan="2">Litter input</td><td colspan="2">-0.13</td><td colspan="2">-0.22</td><td colspan="2">0.02</td></tr>
<tr><td colspan="2">Broadleaf percentage</td><td colspan="2">0.19</td><td colspan="2">-0.57</td><td colspan="2">-0.02</td></tr>
<tr><td colspan="8">Importance of components</td></tr>
<tr><td colspan="2">Standard deviation</td><td colspan="2">1.89</td><td colspan="2">1.33</td><td colspan="2">1.18</td></tr>
<tr><td colspan="2">Proportion of variance</td><td colspan="2">0.36</td><td colspan="2">0.18</td><td colspan="2">0.14</td></tr>
<tr><td colspan="2">Cumulative proportion</td><td colspan="2">0.36</td><td colspan="2">0.53</td><td colspan="2">0.67</td></tr>
<tr><td rowspan="3">SOC stocks</td><th colspan="7">ANOVA analysis incl. PC1, PC2, and PC3</th></tr>
<tr><td rowspan="2">Residual (adj. R^2)</td><th colspan="2">PC 1</th><th colspan="2">PC 2</th><th colspan="2">PC 3</th></tr>
<tr><td>SS</td><td>F</td><td>SS</td><td>F</td><td>SS</td><td>F</td></tr>
<tr><td>Organic layer</td><td>70.5 (0.29)</td><td>19.6</td><td>$F_{(1,471)}$= 115.7 ***</td><td>9.9</td><td>$F_{(1,471)}$= 58.9 ***</td><td>-</td><td>-</td></tr>
<tr><td>Total SOC stocks</td><td>80.1 (0.19)</td><td>4.2</td><td>$F_{(1,416)}$= 21.9 ***</td><td>2.2</td><td>$F_{(1,416)}$= 11.5 ***</td><td>13.5</td><td>$F_{(1,416)}$= 70.4 ***</td></tr>
<tr><td>Residual SOC stocks</td><td>83.2 (0.16)</td><td>1.0</td><td>$F_{(1,416)}$= 5.1 *</td><td>-</td><td>-</td><td>15.8</td><td>$F_{(1,416)}$= 78.9 ***</td></tr>
</table>

3.2. Measured SOC stocks and its explanatory variables

Measured total SOC stocks were highest in the Southern Alps (17.0±1.5 kg C m^{-2}) followed by the Pre-Alps, Jura, Alps and the Swiss Plateau ($P_{Region}<0.001$; *Fig. 2*). Furthermore, conifer forests stored more C in the organic layer than broadleaf forests (3.6±0.3 vs. 0.9±0.1 kg C m^{-2}). As SOC stocks in the mineral soil layer did not differ significantly between the two forest types, total SOC stocks were greater in the conifer than in the broadleaf forests (13.7±0.6 vs. 10.4±0.3 kg C m^{-2}). Furthermore, there was no difference in SOC storage between acidic and calcareous soil (11.4±0.4 vs. 11.6±0.4 kg C m^{-2}), whereas waterlogged soils had higher SOC stocks (15.5±1.2 kg C m^{-2}) than non-waterlogged soils ($P<0.005$).

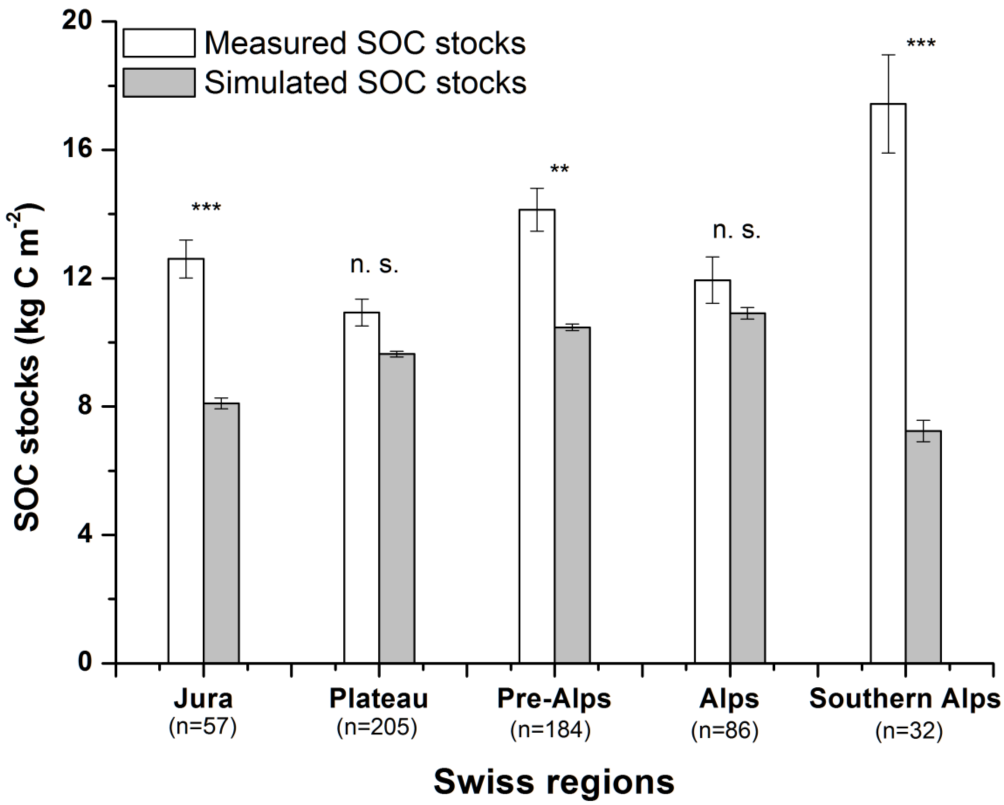

Fig. 2: Comparison between measured and simulated SOC stocks in the five biogeographic regions of Switzerland. Data are represented as means ±standard errors.

Litter inputs derived from the NFI showed a small but significant decrease with increasing elevation (-0.40±0.11 kg C $m^{-2}y^{-1}$ per 1000 m elevation gain; r^2=0.02***; *Fig. 3a*) correlating with decreasing wood removal from the forest as harvesting rates decline with elevation (Brändli, 2010). The estimated non-woody litter amounted on average to 70% of the total litter input. In contrast to the litter, C in the organic layer increased with elevation (3.3±0.4 kg C $m^{-2}y^{-1}$ per 1000 m in altitude; r^2=0.12***, *Fig. 3b*). In the mineral soil, SOC stocks remained constant with altitude (*Fig. 3c*), indicating that the ratio between SOC stored in the organic layer and in the mineral soil also increased with altitude (*Figs. 3b and 3c*). The effect of litter input on total SOC stocks was significant but explained only little of the total model variance (*Table 3*).

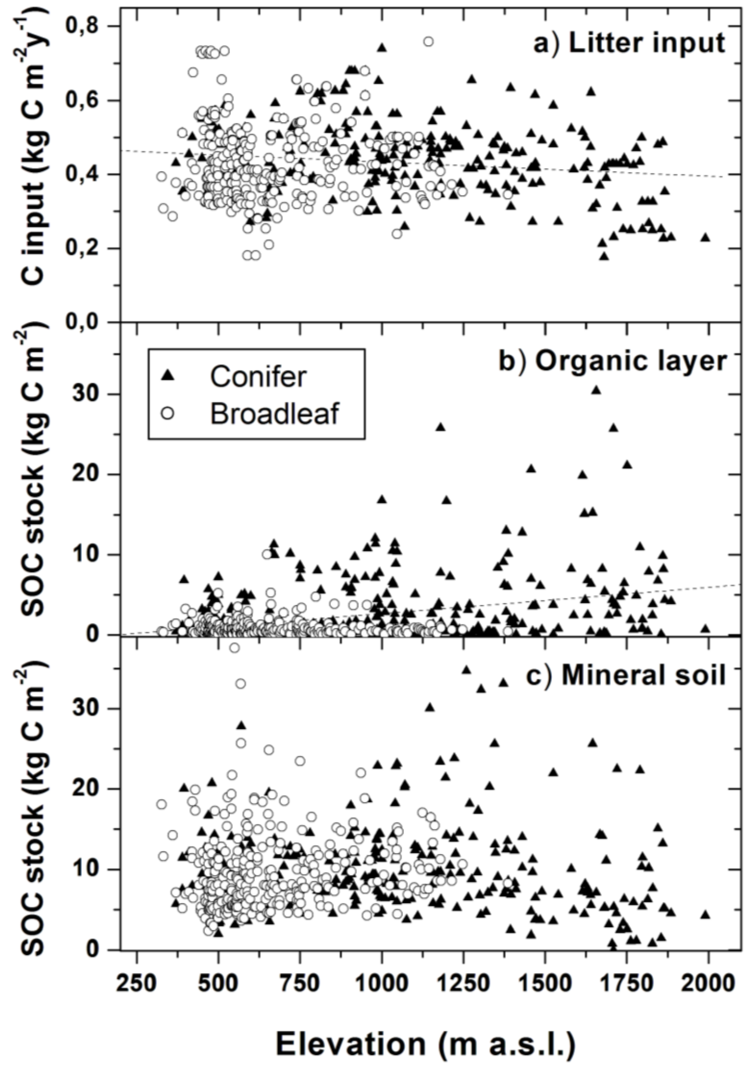

Fig. 3: Litter-derived C inputs (3a) and SOC pools in the organic layer (3b) and in the mineral soil (at soil depth 0-100 cm, 3c) in relation to elevation across Switzerland. The upper graph shows the mean values of litter inputs (sum of woody and non-woody litter) for a period of 30 years. Circles represent broadleaf forests; triangles represent conifer ones. Lines represent linear regression fits when significant.

PC1 (primarily soil chemistry) and PC3 (primarily MAP and clay) explained the most variance for total SOC storage (both $P<0.005$). In comparison, PC2 (mainly MAT and forest type) explained significant amounts of variation in organic layer C stocks but not in total SOC stocks (*Table 2*). The gls model revealed that soil type, exposition, and relief had no explanatory power on SOC stocks and were therefore not included in the ANOVA model. Finally, the set of explanatory variables fed into the ANOVA included contents of exchangeable Fe, Al, Ca, pH, slope, MAT, MAP, forest type, litter input, and clay content. In the organic layer, exchangeable Fe was the most important explanatory variable (Sum of Squares (SS), SS = 25.3%), followed by MAT and forest type. For total SOC stocks, the variables with the highest explanatory power were Fe content (SS = 15%, *Fig. 4*) and Ca content (SS = 13%). Furthermore, MAP showed a strong positive relationship with SOC stocks (SS = 5%).

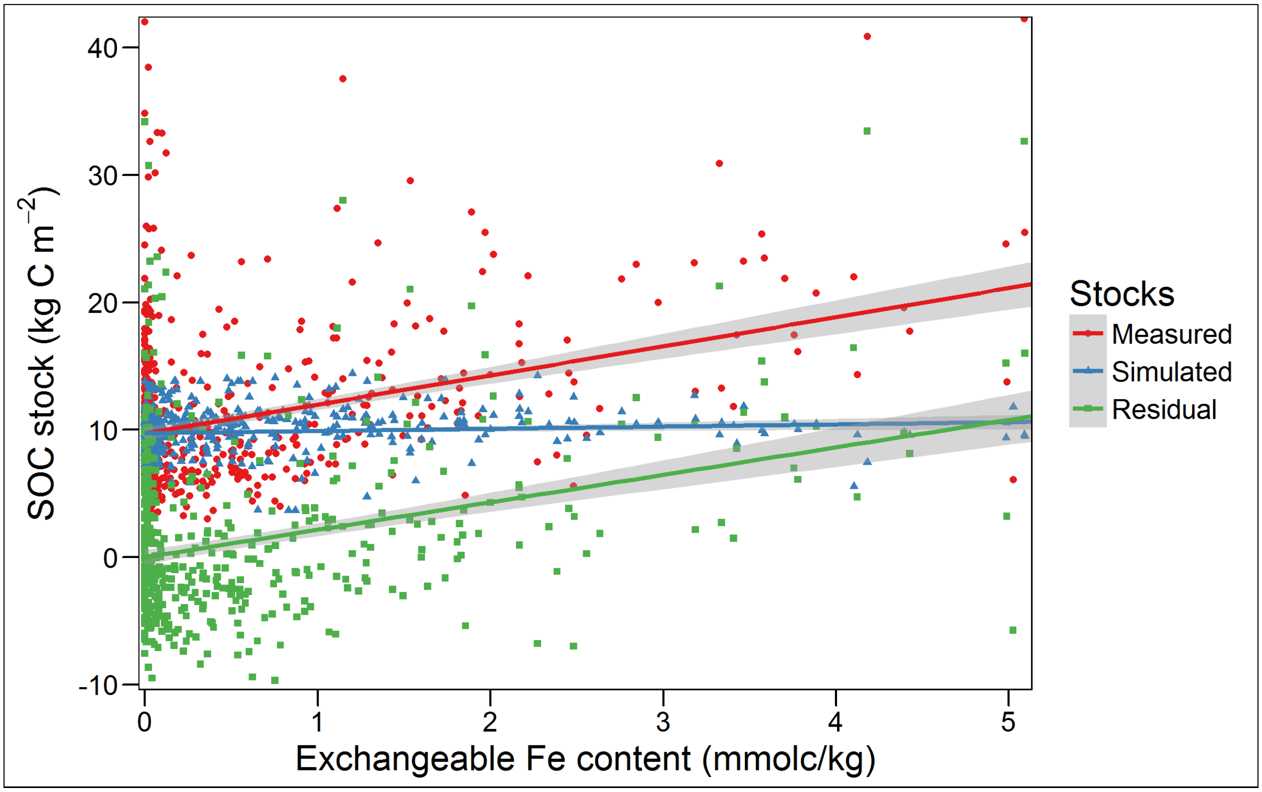

Fig. 4: Effect of exchangeable Fe content (at 0-30 cm soil depth) on measured, simulated, and residual SOC stocks (kg C m^{-2}). Lines are robust linear regression; grey areas represent the confidence intervals.

The overall model explained 37% of the variance (adjusted R^2; *Table 3*). Since in all analyses soil chemical properties predicted large part of the model variances, and as exchangeable Fe and Ca are pH-dependent, we separated the data into subsets of sites with soil samples of pH < 5 and pH > 5. In the subset of pH < 5, the importance of exchangeable Fe increased (SS = 33.8%), whereas exchangeable Ca became more important in the subset of soils with pH > 5 (SS = 20.6%, *Supplementary table 1*). The gls model revealed the effect of the factor region to be based on the particularly high SOC stocks in the Southern Alps which might be at least partly attributed to high contents of fire-derived black carbon (Eckmeier et al., 2010), which was not measured at the national scale. Therefore, the ANOVA was repeated excluding this region. Results showed exchangeable Ca and Fe to be the most important explanatory variables (SS = 15.6% and SS = 11.7%, respectively), and to a lesser degree forest type, slope, and MAP (*Supplementary table 1*).

3.3. Modeling SOC stocks

The Yasso15 model predicted substantially smaller SOC stocks than measured ones (difference in the means of 2.3 kg C m^{-2}; *P<0.005*; *Fig. 2*). In contrast to measured SOC stocks, simulated SOC stocks did not differ considerably among regions, with the greatest SOC stocks simulations in the Alps and the Pre-Alps (11.0±0.2 and 10.5±0.1 kg C m^{-2}, respectively), and the smallest in the Southern Alps (7.2±0.3 kg C m^{-2}). Consequently, the largest difference in SOC stocks were observed in the Southern Alps with an underestimation of almost 10 kg C m^{-2}. Discrepancies were likewise high in the Jura and the Pre-Alps (an underestimation of 4 and 3 kg C m^{-2}, respectively). In comparison, SOC simulations for the Alps and the Swiss Plateau agreed very well with the measurements at the regional scale, with less than one kg C m^{-2} difference in the Swiss Plateau and the Alps, respectively.

Waterlogged soils had substantially smaller modeled than measured SOC stocks in all five regions (*P<0.005*, *data not shown*). However, modeling SOC stocks excluding waterlogged soils (n=89) only slightly affected the discrepancy between modeled and measured SOC stocks (difference in means of 1.8 kg C m^{-2}). In the Pre-Alps, there were two waterlogged sites (Gleysols) with extremely high SOC stocks (65.2 and 63.4 kg C m^{-2}). Excluding these two outliers reduced the observed discrepancy in the Pre-Alps by one kg C m^{-2}.

3.4. Residual analysis

In the ANOVA of discrepancies between measured and modeled SOC stocks, waterlogged soils were excluded. The results showed exchangeable Ca and Fe contents to be related to the measured-modeled residual SOC stocks, explaining 13.8% and 9.5% of the total model variance, respectively (*Table 3*). Residual SOC stock increased with MAP, Fe and Ca contents (all *P<0.005*). Although MAP was included as a climatic parameter in Yasso15, the discrepancies between measured and modeled SOC stocks were greater at high MAP (SS = 5.9%). SOC stock discrepancies were furthermore greater in conifer as compared to in broadleaf forests (3.7±0.6 vs. 1.0±0.4 kg C m^{-2}). Slope showed a significant impact, with larger differences in SOC stocks in flatter than in steep areas. Overall, the ANOVA model of the residuals explained 42% of the variance (*Table 3*).

Table 3: Results from the ANOVA analyses. Tables 3a and 3b present results for measured SOC stocks (entire datasets, waterlogged soils excluded). Tables 3c-3g present data for the measured-simulated residual SOC stocks (waterlogged soils excluded except for table 3g). SS is the sum of squares (in %), and F stands for F value. The sign "-" indicates that a variable was not present in the final model fit as it was removed from the model due to insignificance. The sign "#" indicates a variable was excluded from of the model due to evidence of multicollinearity. The adjusted R^2 is presented in parentheses after the residuals.

Parameter	**Measured SOC stocks**				**Measured-simulated residual SOC stocks**									
	a) Organic layer		**b) Total SOC stocks**		**c) Entire dataset**		**d) pH < 5**		**e) pH > 5**		**f) S. Alps excluded**		**g) Including waterlogged soils**	
	SS (%)	F-value	SS (%)	F-value	SS (%)	F-value	SS (%)	F-value	SS (%)	F-value	SS (%)	F-value	SS (%)	F-value
Fe content	25.3	$F_{(1,415)}$= 155.9 ***	15.0	$F_{(1,413)}$= 100.3 ***	9.5	$F_{(1,410)}$=67.9 ***	26.5	$F_{(1,242)}$=122.9 ***	-	-	5.6	$F_{(1,381)}$= 37.6 ***	6.2	$F_{(1,482)}$= 48.7 ***
Al content	1.1	$F_{(1,415)}$= 6.9 **	#	#	#	#	0.7	$F_{(1,242)}$= 3.3 .	-	-	#	#	#	#
Ca content	4.3		13.4	$F_{(1,413)}$= 89.7 ***	13.8	$F_{(1,410)}$= 98.7 ***	-	-	26.4	$F_{(1,164)}$= 72.1 ***	18.1	$F_{(1,381)}$= 121.2 ***	15.6	$F_{(1,482)}$= 122.1 ***
pH	-	-	-	-	-	-	-	-	1.3	$F_{(1,164)}$= 3.5 .	-	-	-	-
Slope	-	-	1.8	$F_{(1,413)}$= 12.2 ***	1.8	$F_{(1,410)}$= 12.9 ***	-	-	5.7	$F_{(1,164)}$= 15.7 ***	6.2	$F_{(1,381)}$= 41.7 ***	3.8	$F_{(1,482)}$ = 29.9 ***
MAT	2.1	$F_{(1,415)}$= 26.2 ***	-	-	1.4	$F_{(1,410)}$= 10.2 ***	2.6	$F_{(1,242)}$= 11.8 ***	-	-	0.8	$F_{(1,381)}$= 5.3 *	-	-
Litter input	-	-	0.8	$F_{(1,413)}$= 5.5 *	7.3	$F_{(1,410)}$= 52.2 ***	6.6	$F_{(1,242)}$= 30.4 ***	4.9	$F_{(1,164)}$= 13.4 ***	4.4	$F_{(1,381)}$= 29.6 ***	3.4	$F_{(1,482)}$ = 26.8 ***
Forest type		$F_{(1,415)}$= 12.7 ***	2.1	$F_{(1,413)}$= 14.2 ***	2.5	$F_{(1,410)}$= 17.7 ***	2.5	$F_{(1,242)}$= 11.5 ***	1.6	$F_{(1,164)}$= 4.3 *	4.8	$F_{(1,381)}$= 32.2 ***	0.4	$F_{(1,482)}$ = 2.9 .
Clay content	-	-	-	-	0.7	$F_{(1,410)}$= 5.1 *	-	-	-	-	-	-	-	-
MAP	-	-	5.0	$F_{(1,413)}$= 33.3 ***	5.9	$F_{(1,410)}$= 42.5 ***	8.6	$F_{(1,242)}$= 39.8 ***	-	-	3.3	$F_{(1,381)}$= 22.5 ***	8.7	$F_{(1,482)}$ = 68.0 ***
Residuals **(R^2)**	67.2 (0.32)	-	61.9 (0.37)	-	57.1 (0.42)	-	52.5 (0.46)	-	60.1 (0.38)	-	56.8 (0.42)	-	61.9 (0.37)	-

In the residual analysis of all soils with a pH < 5, Fe and MAP explained a large part of the total model variance (SS = 26.5% and SS = 8.6%, respectively), whereas in the subset of pH > 5, Ca content and slope explained 26.4% and 5.7%, respectively (*Table 3*). The explanatory power of exchangeable Fe content remained high (SS = 5.6%) when Southern Switzerland was excluded, but Ca content explained more of the total model variance (SS = 18.1%). Whereas, slope predicted 6.2% of the model variance, the explanatory power of MAP decreased (SS = 3.3%).

Linear regressions of the key explanatory variables with residual SOC stocks yielded the following equations for a potential correction with y being the SOC stock: SOC=0.0004 Fe [mmolc/kg] – 0.1203 (R^2=0.06) and SOC=0.0576 Ca + 145.75 (R^2=0.03); SOC=-0,0071 MAP [mm y^{-1}] + 109,19 (R^2=0.01).

4. DISCUSSION

Our study showed that SOC stocks in mature forests in Switzerland are predominantly related to SOM stabilizing properties in soils, in particular exchangeable Fe and Ca, and to a smaller extent to precipitation (MAP). In contrast, litter inputs had only a negligible statistical influence on SOC storage, while forest type was of primary importance for SOC stocks in the organic layer. The litter decomposition model Yasso estimated SOC stocks adequately for three out of five biogeographical regions although the modeling based on litter inputs was conducted at a larger scale than the quantification of SOC stocks at the profile scale. However, Yasso systematically underestimated SOC stock in the Jura and Southern Alps, which was most closely related to exchangeable Fe and Ca contents. These findings show that SOM stabilization plays a key role for SOM storage, which is not represented in the litter decomposition model.
Sorption to mineral surfaces is one of the key stabilization mechanisms of SOM in soils (e.g. Kaiser and Guggenberger, 2003; Kleber et al., 2007). The nature of sorption, however, depends on soil pH, with SOM being most closely associated with Fe-oxides at low pH values, whereas Ca-carbonates dominate as adsorbents at high pH values (Oades, 1988; Gocke et al., 2011; Lopez-Sangil and Rovira, 2013). This pattern is also reflected at the Swiss national scale (*Fig. 4; Table 3*). Exchangeable Fe content was the most important driver for SOM storage, especially at pH values below 5, where Fe becomes exchangeable and Fe-oxides prevail (Huang and Hardie, 2011). Fe also explained most of the variance in the discrepancies between measured and modeled SOC stocks, which were particularly large in the Southern Alps, with high contents of pedogenic oxides (Blaser et al., 1997) and high SOC stocks averaging 17 kg C m^{-2}. For Southern Switzerland, Eckmeier et al., (2010) have additionally attributed the high SOC stocks to large contents of stable black carbon derived from frequently occurring forest fires. In our national scale study, we were not able to identify the potential contribution of black carbon. However, the additional analysis of the dataset without the soil profiles from Southern Switzerland showed a similarly dominant influence of exchangeable Fe on the measured-modeled SOC stock residuals. Due to the low solubility product of Fe-oxides, Fe extracted with NH_4Cl comprises Fe^{2+} and/or organically bound, colloidal Fe(III)-cations (Schwertmann et al., 1987). Exchangeable Fe may, however, serve as an indicator for the contents of Fe-oxides as indicated by significant correlations of NH_4Cl-extractable Fe with poorly-cristalline Fe-oxides (oxalate-extractable) and organically-bound Fe (pyrophosphate-extractable) for a subset of surface soils,

where Fe-oxides had been measured (*Supplementary Fig. 1*). Stabilization of SOC might also be related to Al-oxides and –hydroxides, which did not appear in the final ANOVA as it co-varies with exchangeable Fe.

For soils with higher pH values (> 5), exchangeable Ca became the most important explanatory variable for both the measured SOC stocks and the residuals with modeled SOC stocks. Calcium is known to bridge negatively charged SOM with negatively charged clay surfaces, thus reducing the access of SOM for decomposers (Oades, 1988). Furthermore, Ca may precipitate with SOM by forming insoluble complexes after reducing the negative charge of the dissolved organic molecules (Oste et al., 2002). Moreover, soil carbonates can enclose organic matter and protect it from decomposition (Gocke et al., 2011). However, exchangeable Ca is (similar to exchangeable Fe) only an indirect measure for $CaCO_3$. In our dataset, there was a highly significant relationship between exchangeable and HNO_3-extractable Ca for a large subset of soils (topsoils, R^2=0.69, n=1033; *unpublished data*) and we thus considered extractable Ca as a representative measure for the carbonate content. In agreement with the stabilization concept, clay contents exerted also a significant influence on SOM stocks at the national scale. The stabilization effect by clay, however, might also be attributed to Fe-oxides occurring in the clay fraction (Dümig et al., 2014).

The positive relation between precipitation and SOC stocks is consistent with the study of (Wiesmeier et al., 2013) in Bavaria with similar environmental conditions as in the northern part of Switzerland. Precipitation could affect SOM storage either directly by inhibiting decomposition, or indirectly by influencing below and aboveground net primary productivity of forest stands and hence C inputs into soils. The comparison of measured and modeled SOC stocks by Yasso15 suggests that a suppressed decomposition is partly contributing to the higher C storage at a high precipitation regime. Yasso is driven by empirically estimated litter inputs from the Swiss NFI and hence should account for productivity effects. However, the model underestimated SOM stocks in regions with high precipitation, strongly suggesting that decomposition is not reflected appropriately, potentially due to anaerobic conditions at the microscale (Hagedorn et al., 2000) or through impeded drainage at the profile or plot scale. The strong underestimation of SOC stocks in waterlogged soils with macroscopic signs of anaerobic conditions in Gleysols and Pseudogleys support the idea that accounting for a reduced drainage would improve the model performance. In addition to precipitation effects on the biological activity of the plant and soil system, precipitation is closely associated with weathering. For instance, in our dataset in Swiss forest soils, MAP appeared on the same axis of the PCA as clay and there is a positive relationship between exchangeable Fe and MAP, suggesting that MAP exerts an indirect influence on SOC stocks through its effect on the reactivity of mineral surfaces. In a Hawaiian study of rain forest soils, Marin-Spiotta et al., (2011) observed that the combination of high rainfalls and oxalate-extractable minerals contributes to SOC sequestration. MAP was less important for SOC storage in soils below a pH of 5, in which Fe was the most important explanatory variable *(Supplementary table 1).*

Relative to MAP, MAT exerted a smaller control on total SOC stocks but a greater one on the organic layer. Part of the negative relationship between MAT and organic layer stock can be attributed to the increasing contribution of conifers with increasing elevation and hence decreasing temperatures (*Fig. 3b*). Though weaker this relationship was still highly significant in conifer forests only. This pattern indicates that SOM quality at the profile scale is affected by MAT with a decreasing contribution of SOM bound to the mineral soil as compared to the 'particulate' SOM in the organic layer. Our results are consistent with the findings of increasing fractions of particulate OM with increasing elevation in grasslands (Leifeld et al., 2009; Budge et al., 2011), which was attributed to a decreasing biological activity with decreasing temperatures. A reduced density and activity of earthworms in high elevation forests might be of particular importance (Bernier, 1996) as bioturbation 'impedes' the accumulation of an organic layer. The greater amounts of labile C at higher altitudes makes them potentially more vulnerable to environmental changes (Hagedorn et al., 2010c).

Topography might be another factor influencing SOC stocks due to soil erosion on steep slopes and waterlogging in flat areas with high clay contents (Fernández-Romero et al., 2014). For forest soils in Ireland, Black et al., (2014) have also shown that the inclusion of topographical factors significantly improved the modeling of SOC stocks using an earlier version of the model (Yasso05). In Swiss forests, we have indeed observed greater SOC stocks at the foot of slopes and in flat areas. However, we attribute the slope effect primarily to waterlogging in soils with a flat slope, because the importance of the explanatory power of slope decreased after removing the waterlogged soils from the statistical and residual analysis.

4.1. Yasso underestimates SOC stocks

At the scale of individual soil profile sites, we expected to find differences between measured and modeled SOC stocks due to the different spatial scales the two approaches are operating at. Whereas SOM stocks were measured in single soil profiles showing a high spatial variability in SOM stocks and turnover (van der Voort et al., 2016), the model's input data are derived from a larger scale. In our study, litter inputs estimated from the NFI were integrated across greater areas (i.e. within a 5 km radius of a soil profile site; section 2.1). The differences in the spatial structure, however, do not sufficiently explain the systematic underestimation of SOC stocks. This appeared to be predominantly related to chemical stabilization and inhibited drainage that are not included in the model (*Table 3*). Our results are supported by a recent study by Doetterl et al., (2015), who demonstrated that SOC storage is controlled mainly by soil geochemistry and only indirectly by climate.

In our analysis of observed litter and soil C stocks, the drivers of the Yasso15 simulations, temperature and precipitation have been confirmed as important variables. Our results reveal no strong effect of MAT on residual SOC stocks, suggesting that temperature effects are reproduced well by the Yasso model. This is consistent with findings by Didion et al., (2014) who showed that regional environmental gradients in Switzerland, such as the increase in SOC stock with elevation, were reproduced accurately with the previous model version Yasso07. However, our simulations with Yasso15 show that MAP had a strong impact on residual SOC stocks, leading to an underestimating of SOC stocks by 0.5 kg C m^{-2} per 100 mm of increase in precipitation. The discrepancies between modeled and measured SOC stock in areas with high rainfalls are in agreement with the study of de Wit et al., (2006) in Norway. The authors, who used the Yasso07 model, attributed the discrepancy in Norwegian forest to an increasing contribution of understory vegetation with increasing rainfalls and hence an increasing C input into soil, which is not accounted for in Yasso driven by forest inventory data. In contrast to our study, there was an overestimation of the SOC sink in Finland and Norway due to uncertainties in the estimated litter inputs and increasing temperatures in the 2000s (Gärdenäs et al., 2011; Dalsgaard et al., 2016a). However, soil physicochemical properties were not considered in the Norwegian study of boreal forests. Gärdenäs et al., (2011) furthermore state that since soil disturbances due to bioenergy removal measures in the 2000s have not been considered in their estimations, soil emissions possibly have been underestimated. The latest study of SOC stocks in Finland indicated an underestimation of SOC stocks for the southern part of Finland, which was explained by the underestimation of understory litter input and due to omission of the effect of drought on SOM decomposition (Lehtonen et al., 2016). For Swedish forest soils, the Yasso model indicated a minor underestimation of SOC stocks, likely related to small litter inputs (Gärdenäs et al., 2011; Ortiz et al., 2013). In contrast, a recent study also based on the foregoing Yasso07, showed that hydrology superseded the importance of litter inputs for forest SOC stock simulations in some soils in Norway (Dalsgaard et al., 2016b). Furthermore, Tupek et al., (2016) suggest that the consideration of SOC stabilization mechanisms in relation to soil nutrient status would improve model simulations of SOC stocks. Regardless of the model limitations, the Yasso07 model is assumed to produce realistic and accurate estimates of C stock changes in soil, litter and dead wood used in the national GHG inventory report (Didion and Thurig, 2016; FOEN, 2017).

The Yasso model was created with the aim to be used for litter decomposition in forest and other soils worldwide, and hence it requires only litter input and quality as well as climate as variables. Our study identifies that SOM stabilization, as one of the key processes for SOM storage, should be considered in improving Yasso. However, parameters controlling SOM stabilization are frequently not available, at least not at a national scale (Black et al., 2014), hindering their implementation in soil models. Relating the discrepancies between measured and simulated SOC stocks empirically to known parameters might be a first approach. It remains, however, uncertain if simple correction functions based on exchangeable Fe and Ca are applicable for other countries. The underestimation of SOC stocks at high precipitation might be explored (or solved) by coupling Yasso with a soil water model which accounts for waterlogging at the micro- and profile-scale. Tuomi et al., (2011) have already pointed out that in certain ecosystems, such as swamps, the Yasso model cannot be applied. Moreover, it remains uncertain, how SOM stabilization or an altered water regime will affect estimates of changes in SOC stock, which is the primary application of Yasso in GHG inventories.

Finally, in contrast to the geochemical properties, litter inputs were not as strongly related to SOC storage in the organic layer and the mineral soil. The influence of climate was found to be significant but less important than the physicochemical soil properties. Whereas total SOC storage increased with increasing MAP, organic layer stocks decreased with increasing MAT. These findings strongly suggest that the expected climatic changes with higher temperatures and an increasing frequency of drought will induce a decrease in SOC storage, but also a change in SOM quality with a declining contribution of non-mineral bound ‘labile’ SOM.

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7. REFERENCES

Bernier, N., 1996. Altitudinal changes in humus form dynamics in a spruce forest at the montane level. Plant Soil 178, 1–28.

Black, K., Creamer, R.E., Xenakis, G., Cook, S., 2014. Improving forest soil carbon models using spatial data and geostatistical approaches. Geoderma 232–234, 487–499. doi:10.1016/j.geoderma.2014.05.022

Blaser, P., Kernebeek, P., Tebbens, L., Breemen, N.V., Luster, J., 1997. Cryptopodzolic soils in Switzerland. Eur. J. Soil Sci. 48, 411–423.

Braakhekke, M.C., Beer, C., Hoosbeek, M.R., Reichstein, M., Kruijt, B., Schrumpf, M., Kabat, P., 2011. SOMPROF: A vertically explicit soil organic matter model. Ecol. Model. 222, 1712–1730. doi:10.1016/j.ecolmodel.2011.02.015

Brändli, U.-B., Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft (Eds.), 2010. Schweizerisches Landesforstinventar: Ergebnisse der dritten Erhebung 2004 - 2006. Bern.

Braun-Blanquet, J., 1964. Pflanzensoziologie. Springer Vienna, Vienna. doi:10.1007/978-3-7091-8110-2

Budge, K., Leifeld, J., Hiltbrunner, E., Fuhrer, J., 2011. Alpine grassland soils contain large proportion of labile carbon but indicate long turnover times. Biogeosciences 8, 1911–1923. doi:10.5194/bg-8-1911-2011

Coleman, K., Jenkinson, D.S., 2014. RothC-A model for the turnover of carbon in soil.

Dalsgaard, L., Astrup, R., Antón-Fernández, C., Borgen, S.K., Breidenbach, J., Lange, H., Lehtonen, A., Liski, J., 2016a. Modeling Soil Carbon Dynamics in Northern Forests: Effects of Spatial and Temporal Aggregation of Climatic Input Data. PLOS ONE 11, e0149902. doi:10.1371/journal.pone.0149902

Dalsgaard, L., Lange, H., Strand, L.T., Callesen, I., Borgen, S.K., Liski, J., Astrup, R., 2016b. Underestimation of boreal forest soil carbon stocks related to soil classification and drainage. Can J Res 46, 1413–1425. doi:dx.doi.org/10.1139/cjfr-2015-0466

de Wit, H.A., Palosuo, T., Hylen, G., Liski, J., 2006. A carbon budget of forest biomass and soils in southeast Norway calculated using a widely applicable method. For. Ecol. Manag. 225, 15–26. doi:10.1016/j.foreco.2005.12.023

Didion, M., Blujdea, V., Grassi, G., Hernández, L., Jandl, R., Kriiska, K., Lehtonen, A., Saint-André, L., 2016. Models for reporting forest litter and soil C pools in national greenhouse gas inventories: methodological considerations and requirements. Carbon Manag. 7, 79–92. doi:10.1080/17583004.2016.1166457

Didion, M., Frey, B., Rogiers, N., Th?rig, E., 2014. Validating tree litter decomposition in the Yasso07 carbon model. Ecol. Model. 291, 58–68. doi:10.1016/j.ecolmodel.2014.07.028

Didion, M., Thurig, E., 2016. Data on soil carbon stock change, carbon stock and stock change in surface litter and in coarse dead wood prepared for the Swiss GHGI. Swiss Federal Institute for Forest, Snow and Landscape Research WSL / Federal Office for the Environment FOEN, Birmensdorf / Bern.

Doetterl, S., Stevens, A., Six, J., Merckx, R., Van Oost, K., Casanova Pinto, M., Casanova-Katny, A., Muñoz, C., Boudin, M., Zagal Venegas, E., Boeckx, P., 2015. Soil carbon storage controlled by interactions between geochemistry and climate. Nat. Geosci. 8, 780–783. doi:10.1038/ngeo2516

Dümig, A., Veste, M., Hagedorn, F., Fischer, T., Lange, P., Spröte, R., Kögel-Knabner, I., 2014. Organic matter from biological soil crusts induces the initial formation of sandy temperate soils. CATENA 122, 196–208. doi:10.1016/j.catena.2014.06.011

Eckmeier, E., Egli, M., Schmidt, M.W.I., Schlumpf, N., Nötzli, M., Minikus-Stary, N., Hagedorn, F., 2010. Preservation of fire-derived carbon compounds and sorptive stabilisation promote the accumulation of organic matter in black soils of the Southern Alps. Geoderma 159, 147–155. doi:10.1016/j.geoderma.2010.07.006

Fernández-Romero, M.L., Lozano-García, B., Parras-Alcántara, L., 2014. Topography and land use change effects on the soil organic carbon stock of forest soils in Mediterranean natural areas. Agric. Ecosyst. Environ. 195, 1–9. doi:10.1016/j.agee.2014.05.015

FOEN, 2017. Emissionen von Treibhausgasen nach revidiertem CO2-Gesetz und Kyoto-Protokoll, 2. Verpflichtungsperiode (2013–2020). Bundesamt für Umwelt BAFU.

Gärdenäs, A.I., Ågren, G.I., Bird, J.A., Clarholm, M., Hallin, S., Ineson, P., Kätterer, T., Knicker, H., Nilsson, S.I., Näsholm, T., Ogle, S., Paustian, K., Persson, T., Stendahl, J., 2011. Knowledge gaps in soil carbon and nitrogen interactions – From molecular to global scale. Soil Biol. Biochem. 43, 702–717. doi:10.1016/j.soilbio.2010.04.006

Gee, G.W., Bauder, J.W., 1986. Particle-size analysis, in: Methods of Soil Analysis. pp. 383–411.

Gimmi, U., Poulter, B., Wolf, A., Portner, H., Weber, P., B?rgi, M., 2013. Soil carbon pools in Swiss forests show legacy effects from historic forest litter raking. Landsc. Ecol. 28, 835–846. doi:10.1007/s10980-012-9778-4

Gnägi, C., Labhart, T., 2015. Geologie der Schweiz. hep-verlag, Bern.

Gocke, M., Pustovoytov, K., Kuzyakov, Y., 2011. Pedogenic carbonate recrystallization assessed by isotopic labeling: a comparison of 13C and 14C tracers. J. Plant Nutr. Soil Sci. 174, 809–817. doi:10.1002/jpln.200900341

Gosheva, S., Walthert, L., Niklaus, P.A., Zimmermann, S., Gimmi, U., Hagedorn, F., 2017. Reconstruction of Historic Forest Cover Changes Indicates Minor Effects on Carbon Stocks in Swiss Forest Soils. Ecosystems. doi:10.1007/s10021-017-0129-9

Hagedorn, F., Kaiser, K., Feyen, H., Schleppi, P., 2000. Effects of Redox Conditions and Flow Processes on the Mobility of Dissolved Organic Carbon and Nitrogen in a Forest Soil. J. Environ. Qual. 288–297.

Hagedorn, F., Spinnler, D., Bundt, M., Blaser, P., Siegwolf, R., 2003. The input and fate of new C in two forest soils under elevated CO2. Glob. Change Biol. 9, 862–872. doi:10.1046/j.1365-2486.2003.00638.x

Hagedorn, F., Moeri, A., Walthert, L., Zimmermann, S., 2010a. Kohlenstoff in Schweizer Waldböden bei Klimaerwärmung eine potenzielle CO_2 -Quelle | Soil organic carbon in Swiss forest soils ? a potential CO $_2$ source in a warming climate. Schweiz. Z. Forstwes. 161, 530–535. doi:10.3188/szf.2010.0530

Hagedorn, F., Mulder, J., Jandl, R., 2010b. Mountain soils under a changing climate and land-use. Biogeochemistry 97, 1–5. doi:10.1007/s10533-009-9386-9

Hernández, L., Jandl, R., Blujdea, V.N.B., Lehtonen, A., Kriiska, K., Alberdi, I., Adermann, V., Cañellas, I., Marin, G., Moreno-Fernández, D., Ostonen, I., Varik, M., Didion, M., 2017. Towards complete and harmonized assessment of soil carbon stocks and balance in forests: The ability of the Yasso07 model across a wide gradient of climatic and forest conditions in Europe. Sci. Total Environ. 599–600, 1171–1180. doi:10.1016/j.scitotenv.2017.03.298

Huang, P.M., Hardie, A.G., 2011. Role of Abiotic Catalysis in the Transformation of Organics, Metals, Metalloids and Other Inorganics, in: Handbook of Soil Sciences. Properties and Processes. pp. 18–26.

IPCC 2006. Guidelines for National Greenhouse Gas Inventories (No. Chapter 4: Forest Land).

IUSS Working Group, W., 2007. World Reference Base for Soil Resources (No. World Soil Resources Reports No. 103. FAO). Rome.

Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D.W., Minkkinen, K., Byrne, K.A., 2007. How strongly can forest management influence soil carbon sequestration? Geoderma 137, 253–268. doi:10.1016/j.geoderma.2006.09.003

Kaiser, K., Guggenberger, G., 2003. Mineral surfaces and soil organic matter. Eur. J. Soil Sci. 54, 219–236.

Kleber, M., Sollins, P., Sutton, R., 2007. A conceptual model of organo-mineral interactions in soils: self-assembly of organic molecular fragments into zonal structures on mineral surfaces. Biogeochemistry 85, 9–24. doi:10.1007/s10533-007-9103-5

Lehmann, J., Kleber, M., 2015. The contentious nature of soil organic matter. Nature. doi:10.1038/nature16069

Lehtonen, A., Linkosalo, T., Peltoniemi, M., Sievänen, R., Mäkipää, R., Tamminen, P., Salemaa, M., Nieminen, T., Ťupek, B., Heikkinen, J., Komarov, A., 2016. Forest soil carbon stock estimates in a nationwide inventory: evaluating performance of the ROMULv and

Yasso07 models in Finland. Geosci. Model Dev. 9, 4169–4183. doi:10.5194/gmd-9-4169-2016

Leifeld, J., Zimmermann, M., Fuhrer, J., Conen, F., 2009. Storage and turnover of carbon in grassland soils along an elevation gradient in the Swiss Alps. Glob. Change Biol. 15, 668–679. doi:10.1111/j.1365-2486.2008.01782.x

Liski, J., Tuomi, M., Rasinmäki, J., 2009. Yasso07 user-interface manual.

Lopez-Sangil, L., Rovira, P., 2013. Sequential chemical extractions of the mineral-associated soil organic matter: An integrated approach for the fractionation of organo-mineral complexes. Soil Biol. Biochem. 62, 57–67. doi:10.1016/j.soilbio.2013.03.004

Marin-Spiotta, E., Chadwick, O.A., Kramer, M., Carbone, M.S., 2011. Carbon delivery to deep mineral horizons in Hawaiian rain forest soils. J. Geophys. Res. 116. doi:10.1029/2010JG001587

Marschner, B., Brodowski, S., Dreves, A., Gleixner, G., Gude, A., Grootes, P.M., Hamer, U., Heim, A., Jandl, G., Ji, R., Kaiser, K., Kalbitz, K., Kramer, C., Leinweber, P., Rethemeyer, J., Schäffer, A., Schmidt, M.W.I., Schwark, L., Wiesenberg, G.L.B., 2008. How relevant is recalcitrance for the stabilization of organic matter in soils? J. Plant Nutr. Soil Sci. 171, 91–110. doi:10.1002/jpln.200700049

MeteoSwiss, Federal Office of Meteorology and Climatology 2013, 2017a., Monthly and Yearly Mean Temperature: TabsM and TabsY

MeteoSwiss, Federal Office of Meteorology and Climatology 2013, 2017b., Monthly and Yearly Precipitation: RhiresM and RhiresY.

Nussbaum, M., Papritz, A., Zimmermann, S., Walthert, L., 2016. Pedotransfer function to predict density of forest soils in Switzerland. J. Plant Nutr. Soil Sci. 179, 321–326. doi:10.1002/jpln.201500546

Oades, J.M., 1988. The retention of organic matter in soils. Biogeochemistry 5, 35–70.

Ortiz, C.A., Liski, J., Gärdenäs, A.I., Lehtonen, A., Lundblad, M., Stendahl, J., Ågren, G.I., Karltun, E., 2013. Soil organic carbon stock changes in Swedish forest soils—A comparison of uncertainties and their sources through a national inventory and two simulation models. Ecol. Model. 251, 221–231. doi:10.1016/j.ecolmodel.2012.12.017

Oste, L.A., Temminghoff, E.J.M., Riemsdijk, W.H.V., 2002. Solid-solution Partitioning of Organic Matter in Soils as Influenced by an Increase in pH or Ca Concentration. Environ. Sci. Technol. 36, 208–214. doi:10.1021/es0100571

Parton, B., Ojima, D., Del Grosso, S., Keough, C., 2001. CENTURY tutorial. Suppl. CENTURY User's Man.

Peltoniemi, M., Thurig, E., Ogle, S., Palosuo, T., Schrump, M., Wutzler, T., Butterbach-Bahl, K., Chertov, O., Komarov, A., Mikhailov, A., 2007. Models in country scale carbon accounting of forest soils. Silva Fenn. 41, 575.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2017. nlme: Linear and Nonlinear Mixed Effects Models R package version 3.1-131.

Prietzel, J., Zimmermann, L., Schubert, A., Christophel, D., 2016. Organic matter losses in German Alps forest soils since the 1970s most likely caused by warming. Nat. Geosci. 9, 543–548. doi:10.1038/ngeo2732

R Core Team, 2017. R: A language and environment for statistical computing R Foundation for Statistical Computing.

Rantakari, M., Lehtonen, A., Linkosalo, T., Tuomi, M., Tamminen, P., Heikkinen, J., Liski, J., Mäkipää, R., Ilvesniemi, H., Sievänen, R., 2012. The Yasso07 soil carbon model – Testing against repeated soil carbon inventory. For. Ecol. Manag. 286, 137–147. doi:10.1016/j.foreco.2012.08.041

Repo, A., Järvenpää, M., Kollin, J., Rasinmäki, J., Liski, J., 2017. Yasso15 graphical user-interface manual.

Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., K?gel-Knabner, I., Lehmann, J., Manning, D.A.C., Nannipieri, P., Rasse, D.P., Weiner, S., Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. Nature 478, 49–56. doi:10.1038/nature10386

Schrumpf, M., Schulze, E.D., Kaiser, K., Schumacher, J., 2011. How accurately can soil organic carbon stocks and stock changes be quantified by soil inventories? Biogeosciences 8, 1193–1212. doi:10.5194/bg-8-1193-2011

Schwertmann, U., Süsser, P., Nätscher, L., 1987. Protonenpuffersubstanzen in Böden. J. Plant Nutr. Soil Sci. 150, 174–178.

Swiss National Forest Inventory, 2017. NFI. https://www.lfi.ch/index-en.php

Swisstopo, 2011. DEM. Swisstopo. https://www.swisstopo.admin.ch/de/home.html

Tuomi, M., Rasinmäki, J., Repo, A., Vanhala, P., Liski, J., 2011. Soil carbon model Yasso07 graphical user interface. Environ. Model. Softw. 26, 1358–1362. doi:10.1016/j.envsoft.2011.05.009

Tuomi, M., Thum, T., J?rvinen, H., Fronzek, S., Berg, B., Harmon, M., Trofymow, J.A., Sevanto, S., Liski, J., 2009. Leaf litter decomposition? Estimates of global variability based on Yasso07 model. Ecol. Model. 220, 3362–3371. doi:10.1016/j.ecolmodel.2009.05.016

Tupek, B., Ortiz, C.A., Hashimoto, S., Stendahl, J., Dahlgren, J., Karltun, E., Lehtonen, A., 2016. Underestimation of boreal soil carbon stocks by mathematical soil carbon models linked to soil nutrient status. Biogeosciences 13, 4439–4459. doi:10.5194/bg-13-4439-2016

van der Voort, T.S., Hagedorn, F., McIntyre, C., Zell, C., Walthert, L., Schleppi, P., Feng, X., Eglinton, T.I., 2016. Variability in ^{14}C contents of soil organic matter at the plot and regional scale across climatic and geologic gradients. Biogeosciences 13, 3427–3439. doi:10.5194/bg-13-3427-2016

Vesterdal, L., Clarke, N., Sigurdsson, B.D., Gundersen, P., 2013. Do tree species influence soil carbon stocks in temperate and boreal forests? For. Ecol. Manag. 309, 4–18. doi:10.1016/j.foreco.2013.01.017

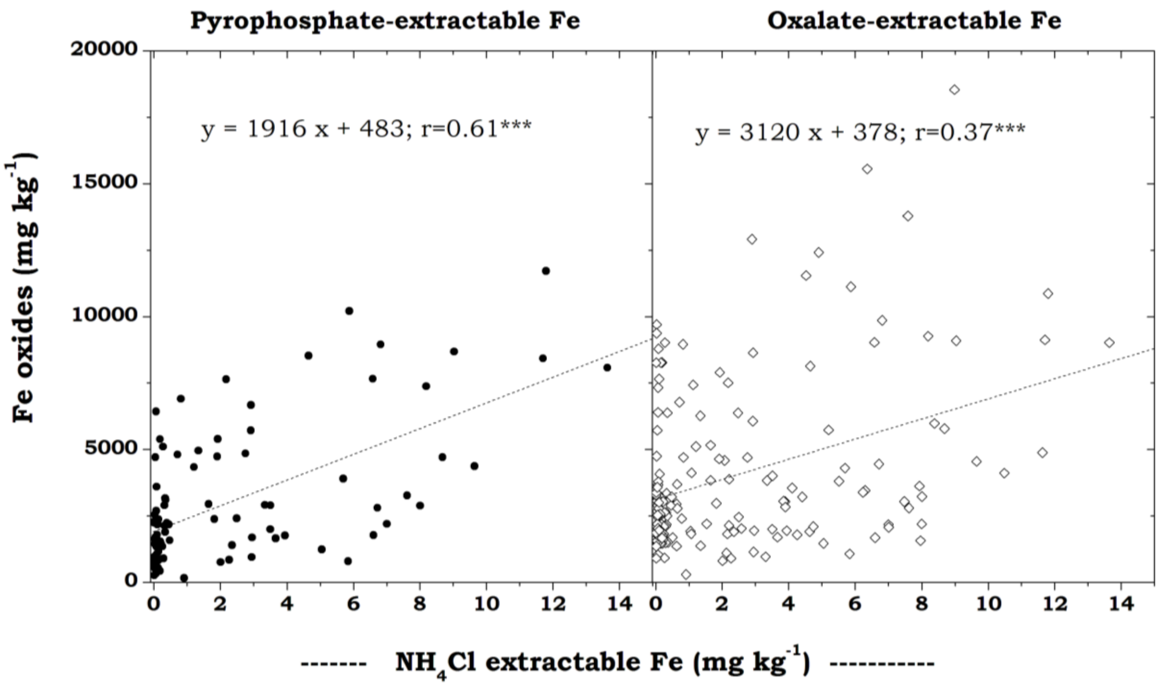
Walthert, L., Graf, U., Kammer, A., Luster, J., Pezzotta, D., Zimmermann, S., Hagedorn, F., 2010. Determination of organic and inorganic carbon, $\delta^{13}C$, and nitrogen in soils containing carbonates after acid fumigation with HCl. J. Plant Nutr. Soil Sci. 173, 207–216. doi:10.1002/jpln.200900158

Walthert, L., Zimmermann, S., Blaser, P., Luster, J., Lüscher, P., 2004. Waldböden der Schweiz. Band 1. Grundlagen und Region Jura. Eidgenössische Forschungsanstalt WSL, Birmensdorf und Hep Verlag, Bern.

Wiesmeier, M., Prietzel, J., Barthold, F., Spörlein, P., Geuß, U., Hangen, E., Reischl, A., Schilling, B., von Lützow, M., K?gel-Knabner, I., 2013. Storage and drivers of organic carbon in forest soils of southeast Germany (Bavaria)? Implications for carbon sequestration. For. Ecol. Manag. 295, 162–172. doi:10.1016/j.foreco.2013.01.025

8. APPENDIX

Supplementary figure 1. Relationship between exchangeable Fe contents extracted with NH4Cl and pedogenic oxides in surface soils (n=167). Pyrophospate-extractable Fe (organically bound Fe-oxides) and oxalate-extractable Fe (poorly crystalline Fe-oxides) were extracted according to (Schwertmann et al., 1987).



Supplementary table 1. Results from ANOVA for the measured SOC stocks (top: organic layer, bottom: total SOC stocks). Results presented include a) subset of dataset with pH <5; b) subset of dataset with pH > 5; c) subset excluding the Southern Alps region, and d) entire dataset including waterlogged soils. Waterlogged soils (n=89) were excluded from all analyses except in d). SS is the sum of squares (in %), and F stands for F value. The sign "-" indicates that a variable was not present in the final model fit as it was removed due to insignificance. The sign "#" indicates a variable was excluded from of the model due to evidence of multicollinearity. The adjusted R^2 is presented in parentheses after the residuals.

Parameter	**Organic layer**							
	a) pH <5		**b) pH >5**		**c) Southern Alps excluded**		**d) Waterlogged soils included**	
	SS (%)	F-value	SS (%)	F-value	SS (%)	F-value	SS (%)	F-value
Fe content	23.1	$F_{(1,245)}$=85.484 ***	3.7	$F_{(1,165)}$= 7.479 **	24.2	$F_{(1,384)}$= 136.677 ***	27.6	$F_{(1,486)}$= 206.896 ***
Al content	-	-	-	-	0.9	$F_{(1,384)}$= 5.302 *	#	#
Ca content	-	-	-	-	-	-	-	-
pH	3.3	$F_{(1,245)}$=12.262 ***	4.0	$F_{(1,165)}$= 8.288 ***	-	-	-	-
Slope	-	-	-	-	-	-	-	-
MAT	3.8	$F_{(1,245)}$=13.85 ***	9.9	$F_{(1,165)}$= 20.394 ***	4.2	$F_{(1,384)}$= 23.97 ***	7.1	$F_{(1,486)}$= 53.252 ***
Litter input	-	-	-	-	-	-	-	-
Forest type	3.5	$F_{(1,245)}$=12.768 ***	-	-	1.8	$F_{(1,384)}$= 10.295 ***	0.5	$F_{(1,486)}$= 3.462 .
Clay content	-	-	1.8	$F_{(1,165)}$= 3.671 .	0.8	$F_{(1,384)}$= 4.65 *	-	-
MAP	-	-	-	-	-	-		
Residuals **(R^2)**	66.3 **(0.33)**	-	80.6 **(0.17)**	-	68.1 **(0.31)**	-	64.8 **(0.35)**	-
Parameter	**Total SOC stocks**							
	a) pH <5		**b) pH >5**		**c) Southern Alps excluded**		**d) Waterlogged soils included**	
	SS (%)	F-value	SS (%)	F-value	SS (%)	F-value	SS (%)	F-value
Fe content	33.9	$F_{(1,246)}$= 144.696 ***	-	-	11.7	$F_{(1,384)}$= 74.205 ***	9.3	$F_{(1,480)}$= 70.446 ***
Al content	-	-	-	-	#	#	#	#
Ca content	-	-	20.6	$F_{(1,164)}$= 50.328 ***	15.6	$F_{(1,384)}$= 98.753 ***	14.8	$F_{(1,480)}$= 111.397 ***
pH	-	-	1.9	$F_{(1,164)}$= 4.851 *	-	-	-	-
Slope	-	-	5.1	$F_{(1,164)}$= 12.491 ***	4.1	$F_{(1,384)}$= 25.928 ***	3.7	$F_{(1,480)}$= 28.283 ***
MAT	-	-	2.3	$F_{(1,164)}$= 5.511 *	-	-	0.7	$F_{(1,480)}$= 5.054 *
Litter input	-	-	-	-	-	-	-	-
Forest type	1.8	$F_{(1,246)}$= 7.616 **	2.9	$F_{(1,164)}$= 6.947 **	4.3	$F_{(1,384)}$= 27.412 ***	1.0	$F_{(1,480)}$= 7.464 **
Clay content	-	-	-	-	-	-	0.5	$F_{(1,480)}$= 3.458 .
MAP	6.8	$F_{(1,246)}$= 29.247 ***	-	-	3.7	$F_{(1,384)}$= 23.196 ***	6.5	$F_{(1,480)}$= 48.872 ***
Residuals **(R^2)**	57.5 **(0.42)**	-	67.2 **(0.31)**	-	60.6 **(0.39)**	-	63.5 **(0.35)**	-

Part C: GENERAL DISCUSSION

5. GENERAL DISCUSSION

My thesis assessed the relative importance of various factors for SOC stocks and quality in Swiss forest soils. The analysis of a large data base of forest soils across Switzerland using statistical approaches, reconstructions of forest history by historical maps, and a litter decomposition model, have contributed to disentangle the factors driving SOM in Swiss forests.

5.1. Tree species composition

Stocks of SOC were closely related to the forest type in the organic layer, but not in the mineral soil, as demonstrated in *Papers I* and *III*. Swiss conifer forests contain nearly four times higher SOC stocks in the organic layer as compared to broadleaf ones (3.8 ± 0.2 vs. 1.0 ± 0.1 kg C m^{-2}, based on a dataset of 857 soil sites). In contrast, SOC stocks in the mineral soil at soil depth of 0-120 cm are almost identical in the two forest types (10.9 ± 0.3 vs. 10.8 ± 0.3 kg C m^{-2}, conifer vs. broadleaf, *Fig. 4*). This suggests that other mechanisms are more important for the SOC stocks in mineral soils, but that the choice of tree species composition is an important determinant for C storage in soils.

The effect of tree species composition on SOC storage has been widely recognized (Jandl et al., 2007; Prescott, 2010; Vesterdal et al., 2013). It can affect SOC stocks in several ways depending on the quality and quantity of the litter input, or the depth of the roots, which all differ between tree species (Jandl et al., 2007). For example, conifer-tree litter contains compounds (e.g. phenols) that are more difficult to decompose than the litter of broadleaf trees (Berg, 2000; Jacob et al., 2010). This promotes the accumulation of a thicker organic layer in conifer trees resulting in higher SOC stocks as compared to broadleaf forests. Since however, the organic layer is considered more labile than the mineral soil, SOC stored under conifer trees could be a potential C source (Vesterdal et al., 2002). Simultaneously, broadleaf forests tend to store the larger part of its SOC stock in the mineral soil and not the organic layer, ensuring a more stable SOC stock (Laganiére et al., 2017). Therefore, numerous studies (Jandl et al., 2007; Prescott, 2010; Vesterdal et al., 2013; Wiesmeier et al., 2013; Schleuß et al., 2014; Liu et al., 2016; Wang et al., 2016) have suggested the establishment of mixed forests as a strategy to promote SOC storage in a changing climate.

Tree species composition was found to be the most important explanatory factor for C/N ratios in European temperate forest soils (Cools et al., 2014) and is subsequently an important driver of SOM stability; lower C/N ratios and higher $\delta^{15}N$ ratios are indicators for greater SOM stability (Kramer et al., 2003). Furthermore, according to a concept by Conen et al., (2008), decreasing C/N ratios and increasing $\delta^{15}N$ ratios can be related to increasing SOM stability. Here, the examination of 54 forest sites separated via density fractionation into different SOM pools (*Paper II*), revealed that firstly, SOM was more stable in the mineral-associated OM as compared to the light fractions and the organic layer; and secondly, that there were differences in fractions according to forest type (*Fig. 7*). The wider ranges detected in the L-F-H horizons as well as the roots measured in the organic layer indicated a forest type dependence in the organic layer. In contrast, no clear differences were detected for the light and heavy fractions, suggesting that the role of tree species composition is less important in mineral soils. One reason for the negligible effect for tree species on SOM in the dense 'stable' SOM-pool could be that mineral associated SOM consists primarily of microbial metabolites and residues which are independent on the parent material (Cotrufo et al., 2013).

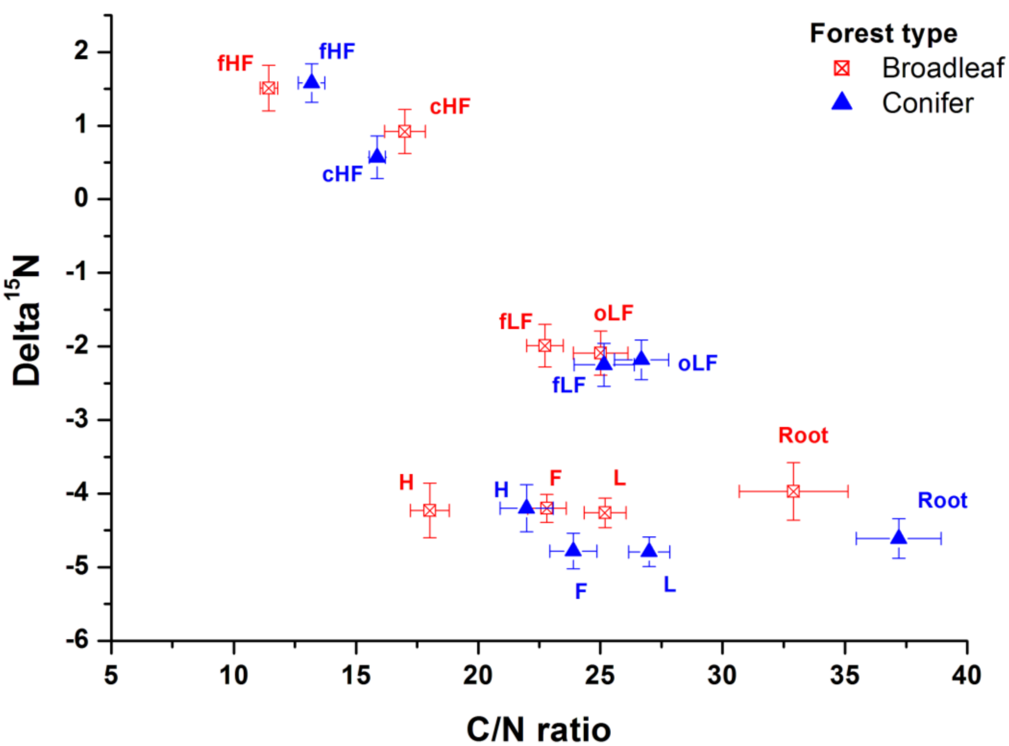


Fig. 7: Isotopic ratio of $\delta^{15}N$ relative to C/N ratio for SOM fractions according to forest type. Organic layer is separated according to L-F-H horizons and roots, which were found in the organic layer. Top mineral soil (0-20 cm) was separated into light (fLF: fine LF and oLF: occluded LF) and heavy (cHF: coarse HF and fHF: fine HF) fractions.

The importance of tree species composition for SOM stability has been emphasized by other studies suggesting that tree species are likely to affect SOM decomposition by influencing soil parameters, known to stabilize SOM (Hobbie et al., 2007) but also that changes in tree species composition (e.g. through incorporating mixed forests in pure forests as suggested by others) could change the chemical stability of SOC through changes in the composition of microbial communities (Wang et al., 2016).

5.2. Climate

Climate was found to be of importance for both SOC stocks and SOM pool distribution in Swiss forest soils. As illustrated in *Paper I*, increased MAT was related to decreased SOC storage in the organic layer, whereas increased MAP was tightly coupled with an increase in mineral soil SOC stocks (*Fig. 8*). The strong effect of climate on SOC storage has been confirmed by other studies with similar site conditions; a repeated soil survey by Prietzel et al., (2016) for example indicated that SOM losses in the Bavarian Alps in Germany are directly related to climate warming. Other studies also demonstrate strong effects of MAP in the Italian Alps (Thuille and Schulze, 2006), and of MAT and MAP in the German Alps (Wiesmeier et al., 2013; Prietzel and Christophel, 2014; Wiesmeier et al., 2014). In addition, a temperate forest study by Meier and Leuschner, (2010) along a precipitation gradient showed that a decrease in precipitation will lead to a decline of SOC storage in both the organic layer and the mineral soils, due to lower rhizodeposition. Precipitation seemed also to be an important factor when simulating SOC stocks, as indicated in *Paper III*. The soil decomposition model Yasso, used to model SOC stocks, showed an underestimation of SOC storage in areas with high precipitation, very likely due to the fact that the model did not account for a suppressed decomposition under anaerobic conditions (Hagedorn et al., 2000). Other studies in Switzerland (Didion and Thürig, 2012) and in Norway (de Wit et al., 2006) have also drawn attention to potential inconsistencies in model simulations at areas with varying climate (such as the Southern Alps, where heavy precipitation events are interrupted by extended drought periods).

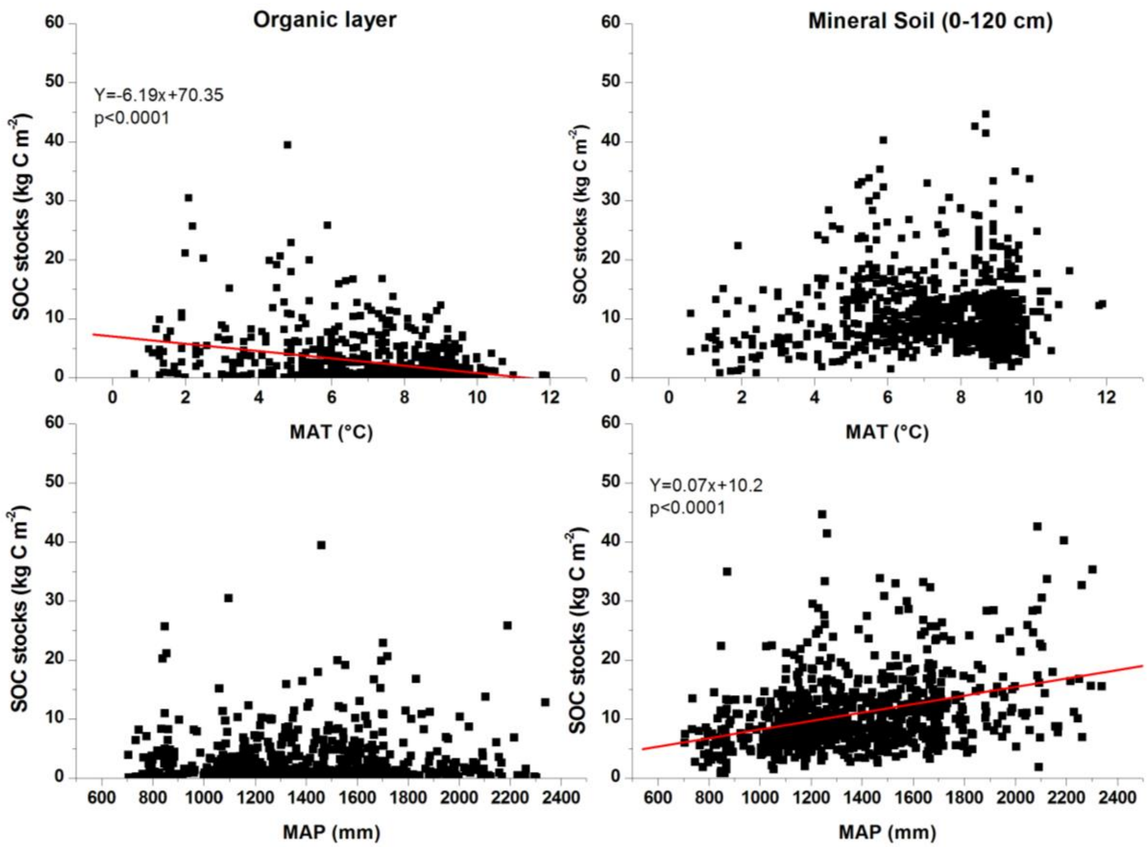


Fig 8: Effect of climate (top: MAT, bottom: MAP) on SOC stocks in the organic layer (left) and the mineral soil (soil depth 0-120 cm, right). Red lines represent linear regression fits when significant.

Climate projections indicate increasing frequency of droughts and more extreme precipitation regimes with high intra-annual variations as well as higher temperatures (Knapp et al., 2008; Stocker, 2013; Frank et al., 2015). Therefore, the pronounced effect of climate, demonstrated in *Papers I* and *III*, and confirmed by other studies, is likely to induce a decrease in SOC storage. The extent of the response of SOC to changes in climate will however differ between the organic layer and the mineral soil, and also depends on additional adaption mechanisms of the plant and soil system. A recent study for example suggested that the degree of ecosystem resilience to climatic changes depends on various factors such as the magnitude and duration of drought as well as tree age (Hagedorn et al., 2016). Also, soil microbial communities respond to soil moisture, with higher abundances of oligotrophic microorganism which may retard SOM decomposition in the long-term (Hartmann et al., 2017).

In addition to affecting SOC stocks, climate was found to affect SOM pool distribution. The examined 54 sites along a natural elevational gradient in *Paper II* did not uncover particularly strong patterns in SOC storage components in relation to climatic conditions. However, total SOC stocks (organic layer + POM + MOM) were highest in warm-moist climatic conditions (14.1 kg C m^{-2} down to 20 cm depth) and lowest in cold-dry climate (9.4 kg C m^{-2}). The contribution of total POM (organic layer + two light fractions) to total SOM was highest in warm-moist climates (72.3%) but lowest in cold-moist climates (62.8%, *Fig. 9*), suggesting a redistribution of SOM pools with decreasing temperatures. This contradicts a grassland study by Leifeld et al., (2009) who found increasing contribution of POM with elevation, corresponding to colder climates. Most likely this is due the differences in the quantity and quality of litter inputs between grasslands and forests. Furthermore, the definition of climatic conditions in *Paper II* could have been responsible for the different POM contribution as cold climate was defined to be colder than 8.51°C, which is relatively modest.

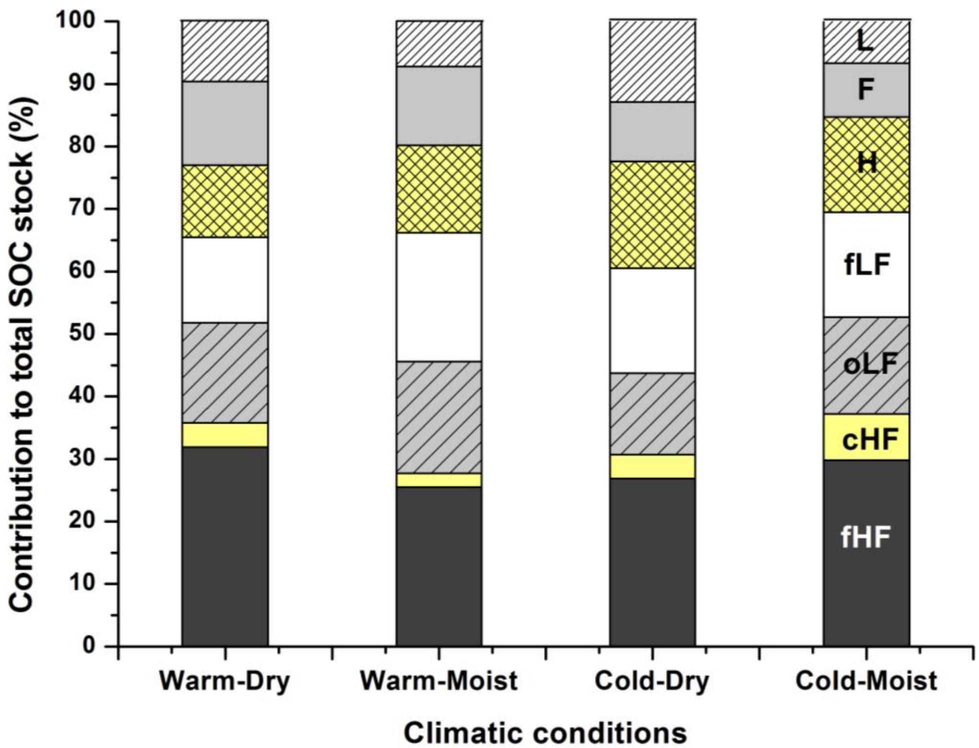


Fig. 9: Contribution of fractions to total SOC stocks according to climatic conditions.

Forest soils store a large amount of the SOM pool in the POM fraction, which is considered to be more vulnerable to changes as compared to the mineral-associated OM. However, some studies suggest that the assumption of labile POM, responding to climate change more strongly than the stable MOM, might be too simple (Davidson and Janssens, 2006) since there is evidence that the two pools do not differ in their response to changes in temperature (Fang et al., 2005).

5.3. Forest cover age

The estimation of the minimal forest cover age of 857 forest soil sites demonstrated that SOC stock of these sites across Switzerland were not strongly influenced by the forest cover age. Based on the evaluation of historical and modern topographic maps, the minimal age of the forest cover was estimated and divided into three forest age classes: forests older than 120 years old (n=567), medium-aged forests between 60 and 120 years (n=219), and forests younger than 60 years of age (n=71). SOC stocks were examined according to these three age categories in *Paper I*. Reflecting the forest age classification, SOC stocks in the organic layer were highest in the medium-aged sites (3.0 ± 0.3 kg C m^{-2}) followed by SOC stocks observed at the young (2.7 ± 0.4 kg C m^{-2}) and the old sites (2.2 ± 0.2 kg C m^{-2}). In the mineral soil, the highest SOC stocks were found in the youngest sites (12.5 ± 0.9 kg C m^{-2}) and decreased with forest age (old < medium < young). Similar results have been found by several other chronosequence studies (Thuille and Schulze, 2006; Poeplau et al., 2011; Hiltbrunner et al., 2013; Guidi et al., 2014), where SOC stocks in the mineral soil decreased after forest expansion. Furthermore, in an attempt to evaluate whether French forest soils are a SOC sink or source, a very recent study concluded that forest SOC accumulation decreases with increasing tree age (Jonard et al., 2017).

In the case of Switzerland, the minor forest age effect with higher SOC stocks in young forests (approximately 1.2-1.7 kg C m^{-2}) as compared to medium and old ones is probably related to the location of the young forest sites. These were generally located on average 200 m higher elevations, having a lower MAT (-0.8°C on average) and higher MAP (+210 mm on average). Under these climatic conditions, higher SOC stocks were inherently greater due to a significant increase of SOC stocks with an increase in MAP in young forests. The most likely reason for the observed small effect of forest age on current SOC storage is due to the previous land use of the youngest sites as grasslands, as grassland soils contain similarly high SOC stocks as forest soils (Schulze et al., 2010; Poeplau et al., 2011). Although, previous land use could not be assessed via the historical maps, Gellrich et al., (2007) estimated for the decade 1980-1990 that reforestation in Switzerland took place predominantly on former alpine pastures and mountainous grasslands. Furthermore, the fact that afforestation in other European countries has occurred to a large extent on former grasslands (Vesterdal et al., 2011) further supports the assumption that afforestation occurred on previous grasslands leading to negligible changes in SOC stocks.

A further contributing factor to the minor age effect is the demonstrated significant impact of forest type on SOC storage in the organic layer (as discussed in *Chapter 5.1.*). The two younger forest age classes had a higher contribution of conifers (55%) as compared to the old forest age class (48%). Although there was no difference in mineral SOC stock between the two forest types, the significantly higher SOC stocks in the organic layer under conifers (on average +2.8 kg C m^{-2}) as under broadleaf forests have contributed to the dominant effect of SOC storage in the two younger forest age classes. The results presented here are in agreement with other studies, such as the study by Wäldchen et al., (2013), which showed no effect of past forest management but a dominant effect by tree species composition.

Although not equally distributed, the classification of sites in three forest categories binned a reasonable number of sites in each forest age category. However, in order to ensure that this classification did not mask any possible age effect, the sites were also separated into five forest age classes with less sites (*Fig. 10*). The more detailed forest age classification showed the same result: SOC stocks decreased with forest cover age.

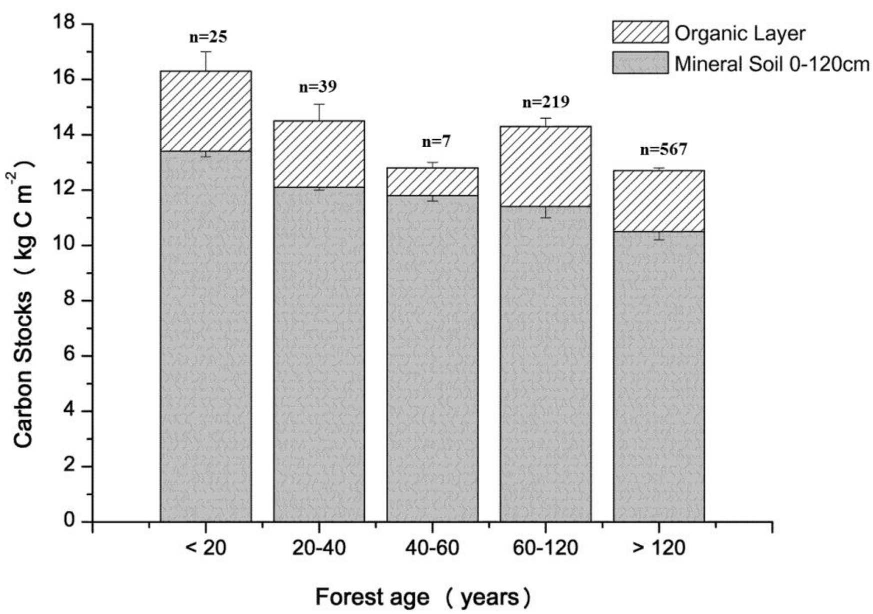


Fig. 10: Distribution of SOC stocks (kg C m^{-2}) according to a more detailed separation of forest age (top dashed: organic layer, bottom grey: mineral soil at 0-120 cm soil depth). Whiskers indicate standard errors, numbers above forest age categories display number of sites per forest age category.

Currently, European temperate forest soils are considered to be a large C sink (Janssens et al., 2003; Luyssaert et al., 2010; Schulze et al., 2010; Pan et al., 2011). Although it is anticipated that afforestation can contribute to further enhancement of SOC storage (Pan et al., 2011), the results of *Paper I* demonstrate that ongoing forest expansion in Switzerland and probably in other mountainous regions of Europe will not likely contribute to soil C sequestration.

5.4. Physicochemical soil properties

SOM storage depends on the C input into soils, its subsequent transformation, and possible stabilization in soils. The interaction of organic compounds with mineral surfaces contributes to a better stabilization of OM into soils and subsequently to SOC accumulation and storage over long periods of time (Marschner et al., 2008; Schmidt et al., 2011). SOM stabilization properties proved to be of key importance for SOC stocks at the Swiss national scale as demonstrated in *Paper II* where soil chemistry was significantly related to the SOM pool distribution and in *Paper III* where extractable Fe and Ca were most closely related to the discrepancies between measured and simulated SOC stocks.

The comparison between measured and simulated SOC stocks using the litter decomposition model Yasso revealed an underestimation particularly in Southern Alps (≈ 10 kg C m^{-2}), known to contain high amounts of pedogenic oxides (Blaser et al., 1997), and in the Jura, which contains high carbonate amounts (*Fig. 11*). A smaller but still considerable underestimate existed in the Pre-Alps (3 kg C m^{-2}) which had the highest contents of extractable Al (but also two waterlogged soils with extremely high SOC stocks, which contributed to the discrepancy). Fe and Al oxides have a high surface areas and reactivity and are known to bind SOM and protect it from decomposition (Oades, 1988; Kaiser and Guggenberger, 2003; Dümig et al., 2014).

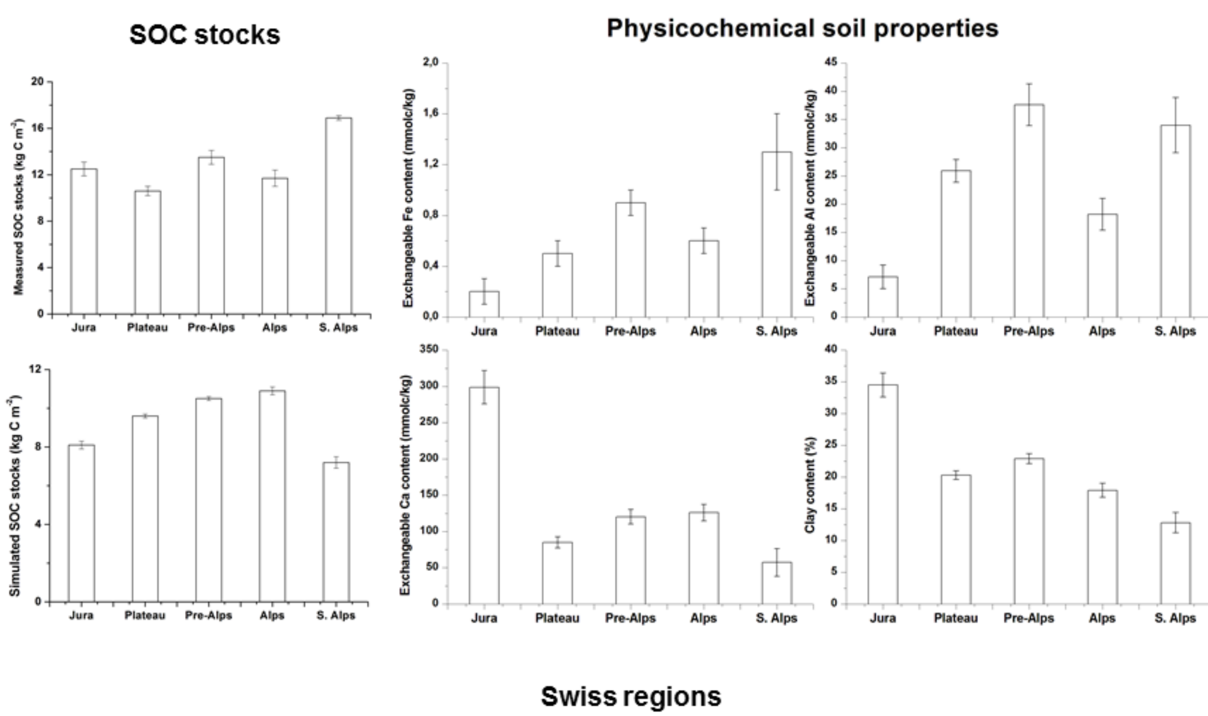


Fig. 11: Physicochemical soil properties according to Swiss biogeographic regions.

Also in the Jura region, containing very high Ca and clay contents, Yasso underestimated SOC stocks (4 kg C m^{-2}). The statistical analysis of the discrepancies between measured and modelled SOC stocks but also of SOC stocks indicated that Ca was closely related to SOC stocks. Calcium is known to stabilize SOM through bridging mechanisms with clay (Oades, 1988) and in carbonates (Gocke et al., 2011).

The effect of soil texture on soil aggregation has been well established (Bronick and Lal, 2005). In particular, higher clay content is associated with higher SOM stability (Plante et al., 2006), therefore clay content is often taken as a proxy of soil aggregation effects on SOM stabilization. The effect of clay content in combination with Ca was visible in the Jura, where SOC stocks were observed to be higher than predicted by model simulations (*Paper III*, *Fig. 11*). Though the sole effect of clay content was weaker as compared to other variables (e.g. pH, Fe-, Al-, Ca-contents), it is necessary to remember that the formation of stable SOM depends on the interaction of clay minerals with pH (Kögel-Knabner et al., 2008), therefore its effect should not be ignored. Overall, the analysis of the Swiss forest soil data base indicated that soils greater SOC stocks are associated with high contents of Fe (Southern Alps), Al (Southern Alps and Pre-Alps) and Ca (Jura). These results are in agreement with the recent study by Doetterl et al., (2015) in South America demonstrating soil geochemistry to be a key determinant of long-term SOC storage and SOM stabilization. Stabilizing minerals and characteristics thus, seem to be key drivers for SOM storage and should be incorporated in SOM models.

5.4.1. Implications of model simulations

Switzerland's commitment to the Kyoto Protocol of the United Nations Framework Convention on Climate Change (UNFCCC) requires to report changes in forests SOC stocks (IPCC, 2006). In general, SOC stock change reporting is based on model simulations due to the unavailability of measurements in most countries (Didion et al., 2016). Swiss reports are based on simulations of the soil C cycling model Yasso, a model specifically developed for forest soils (Hernández et al., 2017), only requiring litter and climate data as model inputs. Although, a main advantage of Yasso is that it requires readily available input data, it also simplifies SOC storage simulations. For example, it assumes that SOM storage depends predominantly on the quantity and quality of litter inputs and on climatic conditions controlling decomposition and 'humification' of SOM. Soil chemistry and soil texture are not well parameterized in current soil carbon models and are therefore not considered when modeling SOM dynamics. The results from *Paper III* however, demonstrate the importance of SOM stabilizing properties and show that SOM stabilization should be implemented in Yasso and other existing belowground models for more accurate predictions.

5.5. Further SOM drivers

Although not assumed main drivers of SOM dynamics, there are further factors contributing to SOC storage. These are described shortly below.

Topography might be another factor affecting SOC storage mainly due to soil erosion on steep slopes and waterlogging in flat areas with high clay contents as observed in Spain (Fernández-Romero et al., 2014). Furthermore, in consideration of Yasso model simulations, Black et al., (2014) demonstrated that the inclusion of topography improves simulations of SOC storage in forest soils in Ireland. In the case of Swiss forest soils, slope, relief, or exposition indicated an importance for SOC storage. However, the effect of relief can be partially attributed to waterlogging in soils (e.g. *Paper III*), as its effect became insignificant once waterlogged soils were excluded from the analysis. Furthermore, during the evaluation of the forest age effect on SOC storage (*Paper I*), the variable 'slope' was of importance as the youngest forest sites were located on steeper slopes at higher elevations as compared to the old forest sites.

Fire-derived OM, the so-called 'black carbon', is the residual of incomplete biomass combustion after a fire (Cotrufo et al., 2016). It is considered very stable and can persist in soils over very long time periods (Marschner et al., 2008; Kuzyakov et al., 2009), making it important for SOC sequestration (Reisser et al., 2016). The Southern part of Switzerland is known to contain large contents of stable black carbon derived from frequently occurring forest fires (Eckmeier et al., 2010), which might have contributed to the extremely high SOC stocks in this region. However, the potential contribution of black carbon could not be quantified in this PhD thesis since the WSL soil database contains no data of black carbon.

There is an emerging concept that SOM stabilization does not only depend on plant polymers but is also affected by microbial communities in soils (Miltner et al., 2012; Kallenbach et al., 2016). An examination of soil microbial communities and their effect of SOC storage, however, goes beyond this PhD thesis and would require an in-depth analysis of hundreds of soil profiles.

6. GENERAL CONCLUSIONS

In this PhD thesis, the main controlling factors of SOM and SOC storage were examined. The main findings are listed below.

6.1. Historical land use change

- *To what extent does the ongoing forest expansion in Switzerland affect SOC storage?*

The results suggest that the ongoing forest expansion in Switzerland will not contribute to an increased sequestration of C in soils.

- *How important is forest age as compared to climate, vegetation, and soil properties?*

The effect of forest age on SOC storage was superimposed predominantly by the effect of climate, forest type, and soil properties.

6.2. SOM pool distribution along climatic gradients

- *How do SOC stocks vary along climatic gradients in Switzerland?*

Climate was clearly less important for SOC stocks than physicochemical soil properties. Along the natural climate gradients, SOC stocks in the mineral soil increased with increasing precipitation, while SOC stocks in the organic layer decreased with increasing temperatures.

- *Does climate have a prominent effect on SOM quality?*

In our study, climate had only a small effect on SOM quality. Similarly as for SOC stocks, SOM pool distribution was most closely related to soil chemistry. Among the climate variables, MAT appeared to be more important than MAP indicated by a closer relation to the pool distribution and the C/N ratios. However, it seems likely that this is an indirect effect through tree species as soils under conifers contained higher contents of particulate organic matter and greater C/N ratios than soils under broadleaf trees.

6.3. The effect of physicochemical stabilization on SOM storage

- *How well does the litter decomposition model Yasso15 predict SOC stocks in Swiss forest soils?*

The newest version of the Yasso model, Yasso15, can predict SOC stocks adequately with small differences in most of the studied regions. However, in regions with high contents of SOM stabilizing minerals as well as in areas with high precipitation, Yasso15 systematically underestimated SOC stocks.

- *Can physicochemical soil properties explain the discrepancies between measured and modeled SOC stocks?*

Results from the comparison of measured and simulated SOC stocks demonstrated that soil properties determining SOM stabilization, specifically exchangeable Fe, Ca, and clay contents, were the main controlling factors of the differences between modelled and measured SOC stocks. Discrepancies also existed but to a lesser extent at high MAP and in waterlogged soils.

These results contribute to the improvement of belowground models to predict SOM responses to future climatic changes. This is in particular relevant for Swiss GHG inventory reporting SOC stock changes, which base their estimations on Yasso simulations.

Key findings of this PhD thesis

Forest type affects SOC stocks in the organic layer.

Forest age only has a minor effect on SOC storage in Swiss forest soils.

SOC storage in the mineral soils increases with increasing MAP, whereas organic layer SOC stocks decrease with increasing MAT.

SOM stabilization plays an important role for SOM storage at the national scale in Switzerland.

7. RESEARCH PERSPECTIVES

When studying SOM storage and SOC dynamics, it is imperative to use a combination of tools to be able to obtain the 'full picture'. Field site experiments help to understand SOM dynamics at a smaller scale, whereas modeling is useful to examine patterns at a large scale and to obtain national wide estimates. *Paper III* demonstrates in a comparison between simulations and measurements of SOC stocks that SOM predictions can improve. However, currently the incorporation of experimental findings into models is challenging. There are a few reasons for this obstacle: firstly, the spatial heterogeneity of soil systems is difficult to parametrize well in models; secondly, our understanding of the complex soil system and processes associated with it is still incomplete and not quantitative; and thirdly, the incorporation of additional parameters into a model depends on the availability of such ones. Large soil databases, such as the one used in this PhD thesis, are extremely rare, mostly due to labor and monetary restrictions. In addition to the spatial scale, a comparison at a temporal scale would be needed to evaluate changes in SOC storage over time. In order to do this, however, repetitive soil sampling is necessary. In the examination of the effect of historical land use changes on SOC storage in *Paper I*, the availability of repetitive soil samples would have enabled a direct temporal comparison in SOC stocks. Furthermore, knowledge of previous land-use of the sites could have contributed to understanding better the minor effect of forest age on SOC storage. Considering the variations in SOC stocks and SOM properties, a comparison of forest sites to grasslands and agricultural sites would have been very interesting with regard to differing driving factors of SOC storage and SOM stabilization. However, a direct comparison is impossible due to differences in soil sampling techniques.

As demonstrated in *Paper I*, historical topographic maps are an useful tool to investigate changes in the forest cover change. Usually, however, there are certain limitations associated with the uncertainty of historical map information; either there are too few maps available or their quality is too poor to assess changes with reasonable certainty. For this reason, the minimal forest age could not be estimated for the entire dataset, and thus some sites had to be removed from the analysis. A possible solution, which however goes beyond the scope of this PhD thesis, is to correct for such inconsistencies by using terrestrial photos as a study by Gimmi et al., (2016) has demonstrated.

Paper II demonstrated that density fractionation can be a useful tool to examine SOM stabilization mechanisms and general trends within soil fractions of different stability. However, due to laborious methodology, it has rarely been applied to soils deeper than the top mineral soils. A notable exception is the study by Schrumpf et al., (2013), which investigated mineral soils down to 60 cm soil depth. Our analysis was restricted to the top 20 cm of the mineral soil.

Since the 54 examined sites were selected according to an ecosystem variability procedure, associated with four climatically different ecosystems, information on SOM stability in deeper soils would have contributed to understanding better the responses of SOM to different climatic conditions.

8. BIBLIOGRAPHY (Parts A & C)

Achat, D.L., Fortin, M., Landmann, G., Ringeval, B., Augusto, L., 2015. Forest soil carbon is threatened by intensive biomass harvesting. Sci. Rep. 5. doi:10.1038/srep15991

Batjes, N.H., 1996. Total carbon and nitrogen in the soils of the world. Eur. J. Soil Sci. 151–163.

Berg, B., 2000. Litter decomposition and organic matter turnover in northern forest soils. For. Ecol. Manag. 133, 13–22.

Black, K., Creamer, R.E., Xenakis, G., Cook, S., 2014. Improving forest soil carbon models using spatial data and geostatistical approaches. Geoderma 232–234, 487–499. doi:10.1016/j.geoderma.2014.05.022

Blaser, P., Kernebeek, P., Tebbens, L., Breemen, N.V., Luster, J., 1997. Cryptopodzolic soils in Switzerland. Eur. J. Soil Sci. 48, 411–423.

Blume, H.-P., Brümmer, G.W., Fleige, H., Horn, R., Kandeler, E., Kögel-Knabner, I., Kretzschmar, R., Stahr, K., Wilke, B.-M., 2016. Scheffer/SchachtschabelSoil Science. Springer Berlin Heidelberg, Berlin, Heidelberg. doi:10.1007/978-3-642-30942-7

Bradford, M.A., Wieder, W.R., Bonan, G.B., Fierer, N., Raymond, P.A., Crowther, T.W., 2016. Managing uncertainty in soil carbon feedbacks to climate change. Nat. Clim. Change 6, 751–758. doi:10.1038/nclimate3071

Brändli, U.-B. (Ed.), 2010. Schweizerisches Landesforstinventar: Ergebnisse der dritten Erhebung 2004 - 2006. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft, Bern.

Braun-Blanquet, J., 1964. Pflanzensoziologie. Springer Vienna, Vienna. doi:10.1007/978-3-7091-8110-2

Bronick, C.J., Lal, R., 2005. Soil structure and management: a review. Geoderma 124, 3–22. doi:10.1016/j.geoderma.2004.03.005

Ciais, P., Sabine, C., Bala, G., Bopp, L., Brovkin, V., Canadell, J., Chhabra, A., DeFries, R., Galloway, J., Heimann, M., others, 2013. Carbon and other biogeochemical cycles, in: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, pp. 465–570.

Ciais, P., Schelhaas, M.J., Zaehle, S., Piao, S.L., Cescatti, A., Liski, J., Luyssaert, S., Le-Maire, G., Schulze, E.D., Bouriaud, O., Freibauer, A., Valentini, R., Nabuurs, G.J., 2008. Carbon accumulation in European forests. Nat. Geosci. 1, 425–430.

Conen, F., Zimmermann, M., Leifeld, J., Seth, B., Alewell, C., 2008. Relative stability of soil carbon revealed by shifts in delta 15N and C:N ratio. Biogeosciences 5, 123–128.

Cools, N., Vesterdal, L., De Vos, B., Vanguelova, E., Hansen, K., 2014. Tree species is the major factor explaining C:N ratios in European forest soils. For. Ecol. Manag. 311, 3–16. doi:10.1016/j.foreco.2013.06.047

Cotrufo, M.F., Boot, C., Abiven, S., Foster, E.J., Haddix, M., Reisser, M., Wurster, C.M., Bird, M.I., Schmidt, M.W.I., 2016. Quantification of pyrogenic carbon in the environment: An integration of analytical approaches. Org. Geochem. 100, 42–50. doi:10.1016/j.orggeochem.2016.07.007

Cotrufo, M.F., Wallenstein, M.D., Boot, C.M., Denef, K., Paul, E., 2013. The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? Glob. Change Biol. 19, 988–995. doi:10.1111/gcb.12113

Crowther, T.W., Todd-Brown, K.E.O., Rowe, C.W., Wieder, W.R., Carey, J.C., Machmuller, M.B., Snoek, B.L., Fang, S., Zhou, G., Allison, S.D., Blair, J.M., Bridgham, S.D., Burton, A.J., Carrillo, Y., Reich, P.B., Clark, J.S., Classen, A.T., Dijkstra, F.A., Elberling, B., Emmett, B.A., Estiarte, M., Frey, S.D., Guo, J., Harte, J., Jiang, L., Johnson, B.R., Kröel-Dulay, G., Larsen, K.S., Laudon, H., Lavallee, J.M., Luo, Y., Lupascu, M., Ma, L.N., Marhan, S., Michelsen, A., Mohan, J., Niu, S., Pendall, E., Peñuelas, J., Pfeifer-Meister, L., Poll, C., Reinsch, S., Reynolds, L.L., Schmidt, I.K., Sistla, S., Sokol, N.W., Templer, P.H., Treseder, K.K., Welker, J.M., Bradford, M.A., 2016. Quantifying global soil carbon losses in response to warming. Nature 540, 104–108. doi:10.1038/nature20150

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173. doi:10.1038/nature04514

de Wit, H.A., Palosuo, T., Hylen, G., Liski, J., 2006. A carbon budget of forest biomass and soils in southeast Norway calculated using a widely applicable method. For. Ecol. Manag. 225, 15–26. doi:10.1016/j.foreco.2005.12.023

Deng, L., Zhu, G., Tang, Z., Shangguan, Z., 2016. Global patterns of the effects of land-use changes on soil carbon stocks. Glob. Ecol. Conserv. 5, 127–138. doi:10.1016/j.gecco.2015.12.004

Didion, M., Blujdea, V., Grassi, G., Hernéndez, L., Jandl, R., Kriiska, K., Lehtonen, A., Saint-André, L., 2016. Models for reporting forest litter and soil C pools in national greenhouse gas inventories: methodological considerations and requirements. Carbon Manag. 7, 79–92. doi:10.1080/17583004.2016.1166457

Didion, M., Thürig, E., 2012. Estimation of carbon stocks and stock changes in soil, LFH layer and deadwood in Swiss forests with Yasso07, Commissioned by the Federal Office for the Environment FOEN. Birmensdorf.

Doetterl, S., Stevens, A., Six, J., Merckx, R., Van Oost, K., Casanova Pinto, M., Casanova-Katny, A., Muñoz, C., Boudin, M., Zagal Venegas, E., Boeckx, P., 2015. Soil carbon storage controlled by interactions between geochemistry and climate. Nat. Geosci. 8, 780–783. doi:10.1038/ngeo2516

Dümig, A., Veste, M., Hagedorn, F., Fischer, T., Lange, P., Spröte, R., Kögel-Knabner, I., 2014. Organic matter from biological soil crusts induces the initial formation of sandy temperate soils. CATENA 122, 196–208. doi:10.1016/j.catena.2014.06.011

Eckmeier, E., Egli, M., Schmidt, M.W.I., Schlumpf, N., Nötzli, M., Minikus-Stary, N., Hagedorn, F., 2010. Preservation of fire-derived carbon compounds and sorptive stabilisation promote the accumulation of organic matter in black soils of the Southern Alps. Geoderma 159, 147–155. doi:10.1016/j.geoderma.2010.07.006

Fang, C., Smith, P., Moncrieff, J.B., Smith, J.U., 2005. Similar response of labile and resistant soil organic matter pools to changes in temperature. Nature 433, 57–60. doi:doi:10.1038/nature03138

FAO (Ed.), 2004. Carbon sequestration in dryland soils, World soil resources reports. Food and Agriculture Organization for the United Nations, Rome.

Fernández-Romero, M.L., Lozano-García, B., Parras-Alcántara, L., 2014. Topography and land use change effects on the soil organic carbon stock of forest soils in Mediterranean natural areas. Agric. Ecosyst. Environ. 195, 1–9. doi:10.1016/j.agee.2014.05.015

Frank, Dorothea, Reichstein, M., Bahn, M., Thonicke, K., Frank, David, Mahecha, M.D., Smith, P., van der Velde, M., Vicca, S., Babst, F., Beer, C., Buchmann, N., Canadell, J.G., Ciais, P., Cramer, W., Ibrom, A., Miglietta, F., Poulter, B., Rammig, A., Seneviratne, S.I., Walz, A., Wattenbach, M., Zavala, M.A., Zscheischler, J., 2015. Effects of climate extremes on the terrestrial carbon cycle: concepts, processes and potential future impacts. Glob. Change Biol. 21, 2861–2880. doi:10.1111/gcb.12916

Fuchs, R., Schulp, C.J.E., Hengeveld, G.M., Verburg, P.H., Clevers, J.G.P.W., Schelhaas, M.-J., Herold, M., 2016. Assessing the influence of historic net and gross land changes on the carbon fluxes of Europe. Glob. Change Biol. 22, 2526–2539. doi:10.1111/gcb.13191

Gee, G.W., Bauder, J.W., 1986. Particle-size analysis, in: Methods of Soil Analysis. pp. 383–411.

Gellrich, M., Baur, P., Zimmermann, N.E., 2007. Natural forest regrowth as a proxy variable for agricultural land abandonment in the Swiss mountains: a spatial statistical model based on geophysical and socio-economic variables. Environ. Model. Assess. 12, 269–278. doi:10.1007/s10666-006-9062-6

Gimmi, U., Ginzler, C., Müller, M., Psomas, A., others, 2016. Assessing accuracy of forest cover information on historical maps. Pr. Geogr. 2016, 718.

Ginzler, C., Brändli, U.-B., Hägeli, M., 2011. Waldflächenentwicklung der letzten 120 Jahre in der Schweiz. Schweiz. Z. Forstwes. 162, 337–343. doi:10.3188/szf.2011.0337

Gocke, M., Pustovoytov, K., Kuzyakov, Y., 2011. Pedogenic carbonate recrystallization assessed by isotopic labeling: a comparison of 13C and 14C tracers. J. Plant Nutr. Soil Sci. 174, 809–817. doi:10.1002/jpln.200900341

Goldhaber, M., Banwart, S.A., 2015. Soil formation, in: Soil Carbon Science Management and Policy by Multiple Benefits. CABI, Oxfordshire UK / Boston, USA.

Guidi, C., Vesterdal, L., Gianelle, D., Rodeghiero, M., 2014. Changes in soil organic carbon and nitrogen following forest expansion on grassland in the Southern Alps. For. Ecol. Manag. 328, 103–116. doi:10.1016/j.foreco.2014.05.025

Guo, L.B., Gifford, R.M., 2002. Soil carbon stocks and land use change: a meta analysis. Glob. Change Biol. 8, 345–360.

Hagedorn, F., Joseph, J., Peter, M., Luster, J., Pritsch, K., Geppert, U., Kerner, R., Molinier, V., Egli, S., Schaub, M., Liu, J.-F., Li, M., Sever, K., Weiler, M., Siegwolf, R.T.W., Gessler, A., Arend, M., 2016. Recovery of trees from drought depends on belowground sink control. Nat. Plants 2, 16111. doi:10.1038/nplants.2016.111

Hagedorn, F., Mulder, J., Jandl, R., 2010a. Mountain soils under a changing climate and land-use. Biogeochemistry 97, 1–5. doi:10.1007/s10533-009-9386-9

Hagedorn, F., Martin, M., Rixen, C., Rusch, S., Bebi, P., Zürcher, A., Siegwolf, R.T.W., Wipf, S., Escape, C., Roy, J., Hättenschwiler, S., 2010b. Short-term responses of ecosystem carbon fluxes to experimental soil warming at the Swiss alpine treeline. Biogeochemistry 97, 7–19. doi:10.1007/s10533-009-9297-9

Hagedorn, F., Spinnler, D., Bundt, M., Blaser, P., Siegwolf, R., 2003. The input and fate of new C in two forest soils under elevated CO2. Glob. Change Biol. 9, 862–872. doi:10.1046/j.1365-2486.2003.00638.x

Hagedorn, F., Kaiser, K., Feyen, H., Schleppi, P., 2000. Effects of Redox Conditions and Flow Processes on the Mobility of Dissolved Organic Carbon and Nitrogen in a Forest Soil. J. Environ. Qual. 288–297.

Hartmann, M., Brunner, I., Hagedorn, F., Bardgett, R.D., Stierli, B., Herzog, C., Chen, X., Zingg, A., Graf-Pannatier, E., Rigling, A., Frey, B., 2017. A decade of irrigation transforms the soil microbiome of a semi-arid pine forest. Mol. Ecol. 26, 1190–1206. doi:10.1111/mec.13995

Hernández, L., Jandl, R., Blujdea, V.N.B., Lehtonen, A., Kriiska, K., Alberdi, I., Adermann, V., Cañellas, I., Marin, G., Moreno-Fernández, D., Ostonen, I., Varik, M., Didion, M., 2017. Towards complete and harmonized assessment of soil carbon stocks and balance in forests: The ability of the Yasso07 model across a wide gradient of climatic and forest conditions in Europe. Sci. Total Environ. 599–600, 1171–1180. doi:10.1016/j.scitotenv.2017.03.298

Hiltbrunner, D., Zimmermann, S., Hagedorn, F., 2013. Afforestation with Norway spruce on a subalpine pasture alters carbon dynamics but only moderately affects soil carbon storage. Biogeochemistry 115, 251–266. doi:10.1007/s10533-013-9832-6

Hiltbrunner, D., Schulze, S., Hagedorn, F., Schmidt, M.W.I., Zimmmermann, S., 2012. Cattle trampling alters soil properties and changes soil microbial communities in a Swiss sub-alpine pasture. Geoderma 170, 369–377. doi:10.1016/j.geoderma.2011.11.026

Hobbie, S.E., Ogdahl, M., Chorover, J., Chadwick, O.A., Oleksyn, J., Zytkowiak, R., Reich, P.B., 2007. Tree Species Effects on Soil Organic Matter Dynamics: The Role of Soil Cation Composition. Ecosystems 10, 999–1018. doi:10.1007/s10021-007-9073-4

IPCC, 2014. Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. Intergovernmental Panel on Climate Change, Geneva, Switzerland.

IPCC, 2006. Guidelines for National Greenhouse Gas Inventories (No. Chapter 4: Forest Land).

IUSS Working Group, W., 2007. World Reference Base for Soil Resources (No. World Soil Resources Reports No. 103. FAO). Rome.

Jacob, M., Viedenz, K., Polle, A., Thomas, F.M., 2010. Leaf litter decomposition in temperate deciduous forest stands with a decreasing fraction of beech (Fagus sylvatica). Oecologia 164, 1083–1094. doi:10.1007/s00442-010-1699-9

Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D.W., Minkkinen, K., Byrne, K.A., 2007. How strongly can forest management influence soil carbon sequestration? Geoderma 137, 253–268. doi:10.1016/j.geoderma.2006.09.003

Janssens, I.A., Freibauer, A., Ciais, P., Smith, P., Nabuurs, G.-J., Folberth, G., Schlamadinger, B., Hutjes, R.W., Ceulemans, R., Schulze, E.-D., others, 2003. Europe's Terrestrial Biosphere Absorbs 7 to 12% of European Anthropogenic CO. Science 1538–1542.

Jobbágy, E.G., Jackson, R.B., 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecol. Appl. 10, 423–436.

Jonard, M., Nicolas, M., Coomes, D.A., Caignet, I., Saenger, A., Ponette, Q., 2017. Forest soils in France are sequestering substantial amounts of carbon. Sci. Total Environ. 574, 616–628. doi:10.1016/j.scitotenv.2016.09.028

Joosten, H., 2015. Current Soil Carbon Loss and Land Degradation Globally: Where are the Hotspots and Why There?, in: Soil Carbon Science, Management and Policy for Multiple Benefits. CABI, Oxfordshire, UK / Boston, USA, pp. 224–235.

Kaiser, K., Guggenberger, G., 2003. Mineral surfaces and soil organic matter. Eur. J. Soil Sci. 54, 219–236.

Kallenbach, C.M., Frey, S.D., Grandy, A.S., 2016. Direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls. Nat. Commun. 7, 13630. doi:10.1038/ncomms13630

Knapp, A.K., Beier, C., Briske, D.D., Classen, A.T., Luo, Y., Reichstein, M., Smith, M.D., Smith, S.D., Bell, J.E., Fay, P.A., Heisler, J.L., Leavitt, S.W., Sherry, R., Smith, B., Weng, E., 2008. Consequences of More Extreme Precipitation Regimes for Terrestrial Ecosystems. BioScience 58, 811. doi:10.1641/B580908

Kögel-Knabner, I., Ekschmitt, K., Flessa, H., Guggenberger, G., Matzner, E., Marschner, B., von Lützow, M., 2008. An integrative approach of organic matter stabilization in temperate soils: Linking chemistry, physics, and biology. J. Plant Nutr. Soil Sci. 171, 5–13. doi:10.1002/jpln.200700215

Kramer, M.G., Sollins, P., Sletten, R.S., Swart, P.K., 2003. N isotope fractionation and measures of organic matter alteration during decomposition. Ecology 84, 2021–2025.

Kümmerle, T., Kaplan, J.O., Prishchepov, A.V., Rylsky, I., Chaskovskyy, O., Tikunov, V.S., Müller, D., 2015. Forest transitions in Eastern Europe and their effects on carbon budgets. Glob. Change Biol. 21, 3049–3061. doi:10.1111/gcb.12897

Kuzyakov, Y., Subbotina, I., Chen, H., Bogomolova, I., Xu, X., 2009. Black carbon decomposition and incorporation into soil microbial biomass estimated by 14C labeling. Soil Biol. Biochem. 41, 210–219. doi:10.1016/j.soilbio.2008.10.016

Laganiére, J., Boca, A., Van Miegroet, H., Paré, D., 2017. A Tree Species Effect on Soil That Is Consistent Across the Species? Range: The Case of Aspen and Soil Carbon in North America. Forests 8, 113. doi:10.3390/f8040113

Lal, R., Lorenz, K., 2012. Carbon Sequestration in Temperate Forests, in: Recarbonization of the Biosphere. Springer Netherlands, Dordrecht. doi:10.1007/978-94-007-4159-1

Lehmann, J., Kleber, M., 2015. The contentious nature of soil organic matter. Nature. doi:10.1038/nature16069

Leifeld, J., Zimmermann, M., Fuhrer, J., Conen, F., 2009. Storage and turnover of carbon in grassland soils along an elevation gradient in the Swiss Alps. Glob. Change Biol. 15, 668–679. doi:10.1111/j.1365-2486.2008.01782.x

Liski, J., Perruchoud, D., Karjalainen, T., 2002. Increasing carbon stocks in the forest soils of western Europe. For. Ecol. Manag. 169, 159–175.

Liu, Y., Li, S., Sun, X., Yu, X., 2016. Variations of forest soil organic carbon and its influencing factors in east China. Ann. For. Sci. 73, 501–511. doi:10.1007/s13595-016-0543-8

Lorenz, K., Lal, R., 2010. Carbon Sequestration in Forest Ecosystems. Springer Netherlands, Dordrecht. doi:10.1007/978-90-481-3266-9

Luyssaert, S., Ciais, P., Piao, S.L., Schulze, E.-D., Jung, M., Zaehle, S., Schelhaas, M.J., Reichstein, M., Churkina, G., Papale, D., Abril, G., Beer, C., Grace, J., Loustau, D., Matteucci, G., Magnani, F., Nabuurs, G.J., Verbeeck, H., Sulkava, M., van der WERF, G.R., Janssens, I.A., members of the CARBOEUROPE-IP SYNTHESIS TEAM, 2010. The European carbon balance. Part 3: forests. Glob. Change Biol. 16, 1429–1450. doi:10.1111/j.1365-2486.2009.02056.x

Marschner, B., Brodowski, S., Dreves, A., Gleixner, G., Gude, A., Grootes, P.M., Hamer, U., Heim, A., Jandl, G., Ji, R., Kaiser, K., Kalbitz, K., Kramer, C., Leinweber, P., Rethemeyer, J., Schäffer, A., Schmidt, M.W.I., Schwark, L., Wiesenberg, G.L.B., 2008. How relevant is recalcitrance for the stabilization of organic matter in soils? J. Plant Nutr. Soil Sci. 171, 91–110. doi:10.1002/jpln.200700049

Meier, I.C., Leuschner, C., 2010. Variation of soil and biomass carbon pools in beech forests across a precipitation gradient. Glob. Change Biol. 16, 1035–1045. doi:10.1111/j.1365-2486.2009.02074.x

Miltner, A., Bombach, P., Schmidt-Brücken, B., Kästner, M., 2012. SOM genesis: microbial biomass as a significant source. Biogeochemistry 111, 41–55. doi:10.1007/s10533-011-9658-z

Moeri, A., 2007. Kohlenstoffvorräte in Schweizer Waldböden mit besonderer Berücksichtigung der organischen Auflage.

Nabuurs, G.-J., Schelhaas, M.-J., Field, C.B., others, 2003. Temporal evolution of the European forest sector carbon sink from 1950 to 1999. Glob. Change Biol. 9, 152–160.

NOAA, 2017. Earth System Research Laboratory Global Monitoring Division.

Nussbaum, M., Papritz, A., Zimmermann, S., Walthert, L., 2016. Pedotransfer function to predict density of forest soils in Switzerland. J. Plant Nutr. Soil Sci. 179, 321–326. doi:10.1002/jpln.201500546

Oades, J.M., 1988. The retention of organic matter in soils. Biogeochemistry 5, 35–70.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.I., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A Large and Persistent Carbon Sink in the World's Forests. Science 333, 988–993. doi:10.1126/science.1204588

Paul, E.A., 2016. The nature and dynamics of soil organic matter: Plant inputs, microbial transformations, and organic matter stabilization. Soil Biol. Biochem. 98, 109–126. doi:10.1016/j.soilbio.2016.04.001

Plante, A.F., Conant, R.T., Stewart, C.E., Paustian, K., Six, J., 2006. Impact of Soil Texture on the Distribution of Soil Organic Matter in Physical and Chemical Fractions. Soil Sci. Soc. Am. J. 70, 287. doi:10.2136/sssaj2004.0363

Poeplau, C., Don, A., Vesterdal, L., Leifeld, J., Van Wesemael, B., Schumacher, J., Gensior, A., 2011. Temporal dynamics of soil organic carbon after land-use change in the temperate zone - carbon response functions as a model approach: SOIL ORGANIC CARBON AND LAND-USE CHANGE. Glob. Change Biol. 17, 2415–2427. doi:10.1111/j.1365-2486.2011.02408.x

Powlson, D., Cai, Z., Lemanceau, P., 2015. Soil Carbon Dynamics and Nutrient Cycling, in: Soil Carbon: Science, Management, and Policy for Multiple Benefits, SCOPE Series. CAB International, Wallingford, Oxfordshire, UK ; Boston, MA, USA.

Prescott, C.E., 2010. Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? Biogeochemistry 101, 133–149. doi:10.1007/s10533-010-9439-0

Preston, C.M., Schmidt, M.W.I., 2006. Black (pyrogenic) carbon: a synthesis of current knowledge and uncertainties with special consideration of boreal regions. Biogeosciences, 397–420.

Prietzel, J., Zimmermann, L., Schubert, A., Christophel, D., 2016. Organic matter losses in German Alps forest soils since the 1970s most likely caused by warming. Nat. Geosci. 9, 543–548. doi:10.1038/ngeo2732

Prietzel, J., Christophel, D., 2014. Organic carbon stocks in forest soils of the German Alps. Geoderma 221–222, 28–39. doi:10.1016/j.geoderma.2014.01.021

Reisser, M., Purves, R.S., Schmidt, M.W.I., Abiven, S., 2016. Pyrogenic Carbon in Soils: A Literature-Based Inventory and a Global Estimation of Its Content in Soil Organic Carbon and Stocks. Front. Earth Sci. 4. doi:10.3389/feart.2016.00080

Remund, J., Rihm, B., Huguenin-Landl, B., 2014. Klimadaten für die Waldmodellierung für das 20. und 21. Jahrhundert Schlussbericht. Bundesamtes für Umwelt BAFU, Bern.

Rigling, A., Schaffer, H.-P., 2015. Forest Report 2015. Condition and Use of Swiss Forests. Federal Office for the Environment / Swiss Federal Institute WSL, Bern / Birmensdorf.

Schleuß, P.-M., Heitkamp, F., Leuschner, C., Fender, A.-C., Jungkunst, H.F., 2014. Higher subsoil carbon storage in species-rich than species-poor temperate forests. Environ. Res. Lett. 9, 014007. doi:10.1088/1748-9326/9/1/014007

Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D.A.C., Nannipieri, P., Rasse, D.P., Weiner, S., Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. Nature 478, 49–56. doi:10.1038/nature10386

Schrumpf, M., Kaiser, K., Guggenberger, G., Persson, T., Kögel-Knabner, I., Schulze, E.-D., 2013. Storage and stability of organic carbon in soils as related to depth, occlusion within aggregates, and attachment to minerals. Biogeosciences 10, 1675–1691. doi:10.5194/bg-10-1675-2013

Schulze, E.D., Ciais, P., Luyssaert, S., Schrumpf, M., Janssens, I.A., Thiruchittampalam, B., Theloke, J., Saurat, M., Bringezu, S., Lelieveld, J., Lohila, A., Rebmann, C., Jung, M., Bastviken, D., Abril, G., Grassi, G., Leip, A., Freibauer, A., Kutsch, W., Don, A., Nieschulze, J., B?Rner, A., Gash, J.H., Dolman, A.J., 2010. The European carbon balance. Part 4: integration of carbon and other trace-gas fluxes. Glob. Change Biol. 16, 1451–1469. doi:10.1111/j.1365-2486.2010.02215.x

Six, J., Conant, R.T., Paul, E.A., Paustian, K., 2002. Stabilization mechanisms of soil organic matter: Implications for C-saturation of soils. Plant Soil 155–176.

Sjögersten, S., Alewell, C., Cécillon, L., Hagedorn, F., Jandl, R., Leifeld, J., Martinsen, V., Schindlbacher, A., Sebastià, M.-T., Van Miegroet, H., 2011. Mountain Soils in a Changing Climate – Vulnerability of Carbon Stocks and Ecosystem Feedbacks, in: Soil Carbon in Sensitive European Ecosystems: From Science to Land Management. John Wiley & Sons, Ltd, Chichester, UK.

Smith, P., Gottschalk, P., Smith, J., 2015. Climate Change and Soil Carbon Impacts, in: Soil Carbon: Science, Management and Policy for Multiple Benefits. CABI, Oxfordshire, UK / Boston, USA, pp. 235–243.

Smith, P., Fang, C., Dawson, J.J.C., Moncrieff, J.B., 2008a. Impact of Global Warming on Soil Organic Carbon, in: Advances in Agronomy. Elsevier, pp. 1–43. doi:10.1016/S0065-2113(07)00001-6

Smith, P., 2008b. Land use change and soil organic carbon dynamics. Nutr. Cycl. Agroecosystems 81, 169–178. doi:10.1007/s10705-007-9138-y

Spielvogel, S., Prietzel, J., Kgel-Knabner, I., 2008. Soil organic matter stabilization in acidic forest soils is preferential and soil type-specific. Eur. J. Soil Sci. 59, 674–692. doi:10.1111/j.1365-2389.2008.01030.x

Stocker, T. (Ed.), 2013. Climate change 2013: the physical science basis: Working Group I contribution to the Fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York.

Swisstopo, 2011. https://www.swisstopo.admin.ch/de/home.html

Tamura, M., Suseela, V., Simpson, M., Powell, B., Tharayil, N., 2017. Plant litter chemistry alters the content and composition of organic carbon associated with soil mineral and aggregate fractions in invaded ecosystems. Glob. Change Biol. doi:10.1111/gcb.13751

Thuille, A., Schulze, E.-D., 2006. Carbon dynamics in successional and afforested spruce stands in Thuringia and the Alps. Glob. Change Biol. 12, 325–342. doi:10.1111/j.1365-2486.2005.01078.x

Torn, M.S., Trumbore, S.E., Chadwick, O.A., Vitousek, P.M., Hendricks, D.M., 1997. Mineral control of soil organic carbon storage and turnover. Nature 389.

van der Voort, T.S., Hagedorn, F., McIntyre, C., Zell, C., Walthert, L., Schleppi, P., Feng, X., Eglinton, T.I., 2016. Variability in ^{14}C contents of soil organic matter at the plot and regional scale across climatic and geologic gradients. Biogeosciences 13, 3427–3439. doi:10.5194/bg-13-3427-2016

Vesterdal, L., Clarke, N., Sigurdsson, B.D., Gundersen, P., 2013. Do tree species influence soil carbon stocks in temperate and boreal forests? For. Ecol. Manag. 309, 4–18. doi:10.1016/j.foreco.2013.01.017

Vesterdal, L., Leifeld, J., Poeplau, C., Don, A., van Wesemael, B., 2011. Land-use change effects on soil carbon stocks in temperate regions – development of carbon response functions, in: Soil Carbon in Sensitive European Ecosystems: From Science to Land Management. John Wiley & Sons.

Vesterdal, L., Ritter, E., Gundersen, P., 2002. Change in soil organic carbon following afforestation of former arable land. For. Ecol. Manag. 169, 137–147.

von Lützow, M., Kögel-Knabner, I., Ekschmitt, K., Flessa, H., Guggenberger, G., Matzner, E., Marschner, B., 2007. SOM fractionation methods: Relevance to functional pools and to stabilization mechanisms. Soil Biol. Biochem. 39, 2183–2207. doi:10.1016/j.soilbio.2007.03.007

Wäldchen, J., Schulze, E.-D., Schöning, I., Schrumpf, M., Sierra, C., 2013. The influence of changes in forest management over the past 200years on present soil organic carbon stocks. For. Ecol. Manag. 289, 243–254. doi:10.1016/j.foreco.2012.10.014

Walthert, L., Graf Pannatier, E., Meier, E.S., 2013. Shortage of nutrients and excess of toxic elements in soils limit the distribution of soil-sensitive tree species in temperate forests. For. Ecol. Manag. 297, 94–107. doi:10.1016/j.foreco.2013.02.008

Walthert, L., Graf, U., Kammer, A., Luster, J., Pezzotta, D., Zimmermann, S., Hagedorn, F., 2010. Determination of organic and inorganic carbon, ? ^{13} C, and nitrogen in soils containing carbonates after acid fumigation with HCl. J. Plant Nutr. Soil Sci. 173, 207–216. doi:10.1002/jpln.200900158

Walthert, L., Zimmermann, S., Blaser, P., Luster, J., Lüscher, P., 2004. Waldböden der Schweiz. Band 1. Grundlagen und Region Jura. Eidgenössische Forschungsanstalt WSL, Birmensdorf und Hep Verlag, Bern.

Wang, H., Liu, S.-R., Wang, J.-X., Shi, Z.-M., Xu, J., Hong, P.-Z., Ming, A.-G., Yu, H.-L., Chen, L., Lu, L.-H., Cai, D.-X., 2016. Differential effects of conifer and broadleaf litter inputs on soil organic carbon chemical composition through altered soil microbial community composition. Sci. Rep. 6. doi:10.1038/srep27097

Wiesmeier, M., Barthold, F., Spörlein, P., Geuß, U., Hangen, E., Reischl, A., Schilling, B., Angst, G., von Lützow, M., Kögel-Knabner, I., 2014. Estimation of total organic carbon storage and its driving factors in soils of Bavaria (southeast Germany). Geoderma Reg. 1, 67–78. doi:10.1016/j.geodrs.2014.09.001

Wiesmeier, M., Prietzel, J., Barthold, F., Spörlein, P., Geuß, U., Hangen, E., Reischl, A., Schilling, B., von Lützow, M., Kögel-Knabner, I., 2013. Storage and drivers of organic carbon in forest soils of southeast Germany (Bavaria) ? Implications for carbon sequestration. For. Ecol. Manag. 295, 162–172. doi:10.1016/j.foreco.2013.01.025

Part D: APPENDIX

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“Are Swiss forest soil carbon stocks resilient to historical land-use?”

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Gosheva S., Walthert L., Niklaus P.A., Zimmermann S., Gimmi U., Hagedorn F. (2017) Reconstruction of Historic Forest Cover Changes Indicates Minor Effects on Carbon Stocks in Swiss Forest Soils. Ecosystems (5) 1:17. DOI: 10.1007/s10021-017-0129-9

Gosheva S., Didion M., Walthert L., Zimmermann S., Oney B.J.,Niklaus P.A., Liski J., Hagedorn F. Disentangling soil organic carbon drivers in forest soils: a model based analysis of the Swiss soil inventory. ***In preparation.***

Gosheva S., Müller M., Walhtert L., Zimmermann S., Niklaus P.A., González Domínguez B.R., Abiven S., Hagedorn F. SOM storage and pool distribution in forest soils along climatic gradients across Switzerland. ***In preparation.***

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